CHAPTER 9

Selection methods Part 1: Organizational aspects of a plant breeding programme

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9.1 INTRODUCTION

The topics covered in this chapter are seldom described in standard plant breeding books, as they arise after the basic choices have been made concerning the breeding programme, such as the choice of germplasm, the choice of the breeding method(s), and the choice of experimental designs and of statistical analysis. We will first analyse the organizational aspects of centralized breeding programmes (CBP), defined as breeding programmes entirely conducted in one or more research stations except for the testing of the final products. We will then examine the organizational aspects in the case of decentralized breeding programmes (DBP): these are defined as breeding programmes in which selection and testing are conducted outside the research station and in the target environment. Subsequently we will discuss the organizational aspects of decentralized-participatory breeding programmes (DPBP), which are defined as breeding programmes in which selection and testing are conducted in the target environment(s) with the participation of the users. One important aspect in the organization of a breeding programme, namely priority setting, has already been discussed in Chapter 4.

9.2 CENTRALIZED BREEDING PROGRAMMES

In the case of a breeding programme conducted entirely on one or more research stations, the organizational aspects are affected by a number of variables, which are both predictable (they tend to come up every year, a typical example being budget changes) and can be addressed within the framework of the research station management, as well as unpredictable variables, such as staff resigning from the job. Several of these variables are common regardless of the type (CBP, DBP or DPBP) of breeding programme.

The organizational aspects that are discussed are:

- land allocation and use (choice of rotations, input levels, depth and time of planting, etc.);
- organization and management of physical resources (equipment);
- organization of human resources (technical staff and labour);
- data capture, storage and analysis; and
- farmer participation in a CBP (farmers visiting and selecting from on-station trials).

9.2.1 Land allocation

One of the major organizational issues in managing a plant breeding programme within a research station is the allocation of land, because, usually, more that one breeding programme operates within the same station, alongside other research programmes, and therefore competition for land is common. The amount of land available to a breeding programme affects a suite of choices ranging from the experimental design, number of replications, plot size and last but not least, the type of rotation under which the material is tested. As nearly all research stations do some type of commercial crop production, the rotation, under which the breeding material is tested, is not chosen based on scientific consideration but on which crops are expected to generate the highest income.

Furthermore, if the only choice left to the breeder is to follow a crop grown for commercial purposes, this also implies testing the breeding material under levels of fertilizers and other agricultural inputs (pesticides, herbicides, etc.) that could be difficult to justify when breeding is for typically low-input crops. Therefore, these organizational issues limit the freedom of the breeder in terms of breeding strategies (for example, the choice of testing the breeding material under a given level of inputs). The only advantage of following a commercial crop on station is that a commercial crop is expected to leave the land highly uniform. However, this is not necessarily true because, for example, the uneven application of inputs can actually create additional sources of uncontrollable variation.

A much better type of organization is when each breeder is allocated two to three times the amount of land needed for the breeding trials and nurseries in a given cropping season to be able to manage, according to their breeding philosophies and strategies, not only the portion of land allocated to current trials and nurseries, but to manage (in terms of rotations and inputs) also the land that will host trials and nurseries in one or two years. This improves considerably the situation compared with the organization described earlier, but it is not without negative aspects. The breeder has often to produce and store, or to purchase, the seed for the cover crops to precede the trials, and has to supervise the agronomic operations to make sure that the complex of rotation and management under which the cover crop is grown represents exactly the conditions under which they intend to test the breeding material.

Even when breeders have full control of the land and of the agronomic operations, the situation on the research station will never be able to represent the variable agronomic situations under which the crop is actually grown by farmers. Often, particularly in developing countries, farmers grow the same crop in a number of different rotations and with different levels of inputs depending on the environment and on the wealth of the farmers and their access to the market. For these reasons, some breeding programmes do extensive evaluation, selection and testing in farmers' fields. Even though the choice of evaluating and testing the breeding material in farmers' fields has nothing to do with participatory plant breeding (PPB) (it could possibly be considered participatory variety selection – PVS), it is expected to have a number of advantages over on-station evaluation, selection and testing. These advantages derive from exposing the breeding material to a multitude of target production areas at an early stage of the breeding programme, assessing the response of different breeding material to a range of different soil types, soil depths, rainfall, agronomic management, etc.

The theoretical framework for discussing response to decentralized selection and more generally the optimum environment for selection, was developed by Falconer (1952, 1981), who demonstrated that selection in the target environment is almost invariably more efficient than indirect selection, i.e. selection in a different environment. This has been confirmed by the theoretical work of Rosielle and Hamblin (1981) and Simmonds (1991), and validated by data from numerous experiments, reviewed by Ceccarelli (1996).

At the same time, the superior efficiency of selecting in target environments has also been disputed by several scientists. However, in the majority of cases (such as Atlin, McRae and Lu, 2000; Rizza *et al.*, 2004; Dodig *et al.*, 2008) this was based on data from a narrow range of yield levels (see also Chapters 2 and 20).

It is important to specify that all breeding programmes have some degree of decentralization in the sense that, sooner or later, the breeding material is tested outside the research station. However, we restrict the use of the term 'decentralized breeding' to mean decentralized selection (Simmonds, 1984), as opposed to decentralized testing, which is commonly the last stage of any breeding programme.

Before we examine the organizational issues associated with a DBP, we need to clarify that a breeding programme is not always taking full advantage of operating in farmers' fields. Cases where the trials are planted in farmers' fields under rotations used in the past but discontinued, or with an unrealistically high level of inputs, or placed at the bottom of a slope where water harvesting effects create a unique micro-environment, indicate that decentralization does not always and invariably mean a higher relevance of the results for the final users.

As we will see later, the management of physical resources is a major issue in participatory breeding programmes dealing with crops or countries with full mechanization, while is much less of an issue with crops or countries where hand operations prevail.

9.2.2 Organization and management of physical resources (equipment)

Similarly to land allocation, physical resources such as vehicles, plot equipment (drills and combines), seed cleaners and seed dressing equipment are in some cases kept in a pool and in other cases assigned specifically to a given breeding programme. The first options is usually favoured by administrators for the most efficient use of physical resources, while the second is favoured by breeders because it avoids additional bureaucratic layers and forms to fill, and it makes sure that the equipment is always available when it is needed. The second option has the advantage of generating a sense of ownership (lacking in the first option), with beneficial effects in terms of care and maintenance.

When the administrators are able to create a healthy working environment with good cooperation between breeding programmes, resulting in sharing and exchanging equipment, the second option can be nearly as efficient as the first one.

9.2.3 Organization of human resources (technical staff and labour)

The management of the human resources (research support staff and labour) associated with a breeding programme is one of the most challenging organizational issues, because the quantity and quality of the work depends largely on their performance. Potential sources of errors are very many in a breeding programme, starting from arranging seed envelopes according to the randomization plan, filling them with seed, planting according to the experimental layout, note taking, harvesting, storing the seed while data are analysed, retrieving the seed of selected entries, and storing the seed till the following planting season. One of key questions in organizing the research support staff around these several tasks is whether to have each staff member assigned to one or more specific task, or to have all of the staff able to perform every operation in the breeding programme.

The first option is usually preferred by the support staff because it is associated with the professional end-of-year evaluation. The major risk associated with this option is the gap of expertise which is created in the case of staff being absent for a long period of time, or even leaving permanently.

The second option has the advantage of greater flexibility in organizing the work and of creating a wider spectrum of prospects should staff leave the breeding programme and apply for other jobs. One exception could be the responsibility for data handling and data management, which is usually the responsibility of a single support staff member, but shared with the breeder(s) (see also the section below).

9.2.4 Data capture, storage and analysis

The traditional manner of organizing data capturing is the manual recording through field books. Field books can be produced using specialized software tools, such as AGROBASE™ (www.agronomix.mb.ca), Excel™ or databases such as Access™. Manual capturing of data has a number of disadvantages, including:

- the preparation of field books is time consuming;
- note taking is weather dependent (field books are very difficult to use on windy or wet days);
- the data are handled twice, being written in the field book first and entered in the computer later, thus increasing the probability of manual errors; and
- the time required for data entry delays statistical analysis, usually until after harvesting, hence reducing the possibility of detecting errors by examining the results of an analysis conducted immediately after the data are collected.

Today data capturing can be easily done electronically using palmtops (there are very many types available on the market) or specifically designed devices, which are usually much more expensive. The file, which will normally be printed as a field book when data capture is by hand, is downloaded into the main memory or in the flash card (recommended) of a palmtop (they usually handle a variety of file types, depending on the brand), which can then be taken to the field to enter data. Electronic data capture has a number of advantages:

- data are entered manually only once and then transferred electronically to the main computer for analysis;
- before leaving the field, it is possible to quickly check the data through sorting and ranking, and immediately correct typing mistakes;
- data can be collected in the field under a wider range of climatic conditions than with field books;
- data analysis can immediately follow data collection, thus providing an additional means of checking for errors in data entry while the crop is still in the field; and
- use of memory cards enables one to keep at hand in the field all the relevant information concerning all trials and nurseries in a large breeding programme.

At the end of the season it is always possible to produce a printout of all the files and to maintain a hard copy of all the data.

Safe data storage is a major issue in plant breeding programmes. Examples of strategies that can be used to reduce to a minimum the risk of data loss are frequent backup; storage of data in external disk drives; and storage of data in at least one computer never connected with networks or the Internet to reduce the probability of introducing viruses.

9.2.5 Farmer participation

Farmer participation in a CBP (farmers visiting and selecting from trials on-station) is not included as a section under PPB because farmers being invited to a station to select between lines, hybrids or clones do not have a chance to develop any sense of ownership of the material they select, which is usually associated with participation in a cyclic, as opposed to linear, process (see also later). Therefore, as noted earlier, farmer participation in a CBP is more akin to PVS than to participatory plant breeding.

As practical experience confirms, farmer selection is environment-dependent (Ceccarelli *et al.*, 2000), so farmers participating in on-station selection should be invited from areas that are similar to the research station in terms of the climatic, agronomic and agricultural systems when the breeding programme has only one station. When the breeding programme has a number of stations simulating a number of different environments, different groups of farmers should be invited to different research stations, unless this activity is part of a research activity involving all farmers making selections on all stations for the sake of comparison.

As farmer visits are usually a single event, the organizational issues involve transportation of the farmers to the station and back, and possibly accommodation for those farmers coming from far away. The logistics can be simplified by inviting only nearby farmers.

Farmers' visits to research stations are a typical activity of the research programmes (not only breeding) in developed countries, where logistic problems are much reduced as farmers are usually able to travel to and from the station by themselves.

If the visit aims at farmers selecting finished or nearly finished varieties, other organizational issues include whether the farmers give a formal score to the breeding material; whether and how the breeders use farmers' preferences as an additional selection criterion; whether and how the material selected is made available to the farmers; and what follow up activity will occur.

9.3 DECENTRALIZED BREEDING PROGRAMMES

Transferring a breeding programme to outside a research station almost always implies losing some degree of control of a number of steps and operations. This is often associated with the perception that less control by scientists is associated with less precision, and this explains the reluctance with which several plant breeders, particularly those in the developing countries, operate away from their research stations.

Within a research station, all the operations associated with running a breeding programme are shared by staff belonging to the same institution and having daily interaction (which does not necessarily make things easier). When a number of stages are transferred outside the research station, a number of operations can, and actually should, be shared with staff belonging to other institutions or to out-posted staff of the same institution, or a combination.

Depending on the presence or absence of a strong extension service, and of the structure of the research institute responsible for the plant breeding, a number of different scenarios are possible.

In the case of countries with a strong extension service and the presence of regional (or subregional or provincial) research centres with infrastructure such as offices, computer facilities, agricultural equipment (including plot machinery), a DBP could be organized based on the following principles:

- The scientist(s) at the institute's headquarters are responsible for the preparations of trials (choice of entries, plot size, experimental design, and having the seed in envelopes ready for planting), the preparation of field books (or electronic files for electronic capture of field data), the preparation of draft field maps with possible alternatives for the layout of the trials, and the shipment of trials with all the detailed instructions for planting and note taking.
- At the headquarters there will be a central database where all the information generated in the breeding programme is kept. Information generated in the regional

centres should also be kept where it was generated as a form of safety duplication.

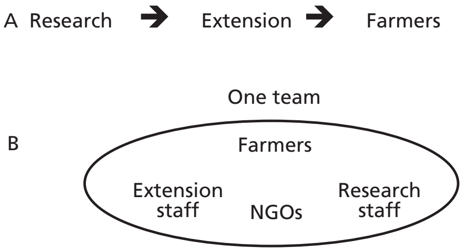
- The main responsibility of the staff of the extension service is to collaborate in the selection of the sites and the specific fields, according to the type and objectives of trials and the general philosophy of the breeding programme.
- The research staff in the regional centres is responsible for implementing the trials on the ground, ensuring the required management, the timing of the field operations and eventually for collecting field data, which are then transferred to headquarters for statistical analysis. Alternatively, when the necessary expertise is available, they can be requested to do the single site analysis, leaving the responsibility for the multi-site analysis to headquarters.
- Extension and research staffs are also responsible for the organization of field days. These are useful not only to show the potential clients the new breeding material, but also to particularly understand through the interaction with farmers whether the experimental setting (location, type of soil, type of management, etc.) is actually representative of farmers' conditions.

This overall organization is facilitated by involving all staff participating in the implementation of the breeding programme in regular meetings, through which the basic principles of the breeding programme are understood and shared by everyone. This obviously includes the full sharing of results among all the participants on an annual basis.

One important beneficial effect of this type of organization is that it replaces the traditional linear sequence of information typical of agricultural research with a continuous flow of information between the different partners (Figure 9.1). As we will see later in this chapter, this concept is fully developed in a participatory breeding programme.

FIGURE 9.1

Replacing the linear sequence Research > Extension > Farmers (A) with continuous flow of information between the different partners (B)



The figure hypothesizes a general situation with a multitude of partners, some of whom may not be present in specific situations.

In this type of scenario, one of the main sources of additional cost associated with decentralized breeding, i.e. transportation and travel, is considerably reduced.

In the case of countries where the extension service is limited or absent, all the responsibilities have obviously to be borne by the research staff.

In describing the organizational aspects of a DBP we are deliberately ignoring the use of additional research stations as 'decentralized' sites, because, even if sub-stations capture differences in temperature and rainfall, they still suffer from all the management issues described earlier, and therefore they may not represent any real production environment.

9.3.1 Countries with only the selection and testing stages of a breeding programme

A special case is that of those countries where, for various, reasons, the national breeding programme cannot afford to go through the first stage of a breeding programme (Chapter 3), i.e. the generation of genetic variability (regardless of the method), and therefore relies entirely on either locally collected germplasm, or on germplasm donated by breeding programmes in other countries or other research centres, such as international agricultural research centres, or by a combination of the two. In such cases, the research station should be used for seed multiplication and also for negative selection, particularly in the case of introduced germplasm, which might have photoperiod or vernalization requirements that makes it ill adapted for national conditions.

Seed multiplication is necessary because the seed from germplasm collections is usually in very small quantities, as it is generally the amount of seed of some of the breeding material received from other breeding programmes.

The steps following the initial seed multiplication depend on the breeding methods and on the type of genetic material received or collected, but will vary from a centralized, on-station, selection evaluation and testing, with only the final stages transferred to farmers fields, to a decentralized programme of the type described above, or to a fully DPBP.

9.4 DECENTRALIZED-PARTICIPATORY BREEDING PROGRAMMES

At the beginning of the chapter we defined participatory plant breeding programmes as breeding programmes in which selection and testing are conducted in the target environment(s) with the participation of the users. Here we will add that, in order to reach its maximum effectiveness, the participation of users should take place as early as possible, and ideally at the beginning of stage two in a plant breeding programme, as described in Chapter 3.

The organizational aspects of a decentralized participatory plant breeding programme do not differ conceptually from those of CBPs. The major difference is that the decisions and the choices for the organizational aspects involve all the stakeholders, and the type of participation depends on how, when and which stakeholders are involved.

We will examine the following organizational aspects:

- Setting criteria to identify target environments and target users.
- Users (different uses of the crop, gender, age, wealth, etc.).
- Locations (representativeness, relevance for the crop, different agroclimatic environments).
- Identification of the target environment and users.
- Type of participation.
- Choice of breeding method.
- Management of trials in farmers' fields.
- Type of genetic material, field layout, machine vs hand operations, data analysis, multi-environment trials (MET).
- Institutionalization of participatory plant breeding.
- The transition phase.

We will not cover here the organizational aspects of Variety release and seed production (Countries with and without a formal seed production system) as these are covered in Chapter 21.

As mentioned earlier, some of these organizational aspects are common to all breeding programmes, while some are specific to a DPBP. At the end of the chapter we will discuss the organizational changes required to migrate from, for example, a centralized non-participatory breeding programme to a DPBP

9.4.1 Setting criteria to identify target environments and target users

A decentralized participatory plant breeding programme may lose a great deal of its potential effectiveness if the sample of both environments and users in which the programme is implemented do not represent both the target environments and the target users. In order to do that, setting the criteria for identification of the target environments and users is a critically important step.

In setting the criteria, it is useful also to assign priorities to the different categories of environments and users so that, depending on the resources available to the programme, environments and users can be added or discontinued on the basis of priorities established in an ideal context.

The most obvious criterion for the choice of the target physical environments, is their representativeness of the major production areas for a given crop (or for the crops covered by the programme) in terms of climatic conditions (temperature, rainfall, elevation), agronomic practices, soil types, landscape, etc. The criteria for the choice of the socio-economic environments are closely interconnected with those of the target users. Therefore the programme has to decide whether to work for all the various socio-economic environments present in the target area, or to privilege the most difficult environments where farmers have fewer opportunities for market access and where most of the agricultural products are used within farms or within the community, or to work only for the most favourable, high potential, environments. It has been argued that PPB has evolved mainly to address the difficulties of poor farmers in developing countries (Ashby and Lilja, 2004) which have been largely bypassed by the products of conventional breeding. In fact there is no reason why the approach should be confined to work with low-income farmers. Basically, when done properly, PPB is an approach that, even if applied in a variety of modes, merges the technical knowledge of the ‘scientists’ with the knowledge of the ‘farmers’, which is historically based on millennia spent in domesticating wild plants and adapting the resulting crops to a multitude of different environments. Therefore, in principle, PPB can apply equally well even in situations of market-oriented agriculture in favourable environments.

The main criteria to identify farmers can be grouped in three broad categories:

- ***Farmer characteristics*** These include language, ethnicity, caste, age, gender, income, education, market relations or orientation, membership of farmer organizations (unions or cooperatives), and relationships among groups within the same community and between communities.
- ***Farmer expertise*** This includes the need to understand whether farmers are already practising some types of plant improvement, as this is essential in the choice of the breeding methodology (see below). In some communities, e.g. Eritrea, specific individuals have specific responsibilities in relation to crop and variety introduction (Soleri *et al.*, 2002).
- ***Farmer needs*** These include the needs of different groups, their perception of risk and hence the type of variety they consider more appropriate in term of stability and yield (Soleri *et al.*, 2002), and the need for special quality attributes either for feed or for food, or both. These include also the farmers’ understanding of production limitations with reference to the use of fertilizers, appropriate rotations and irrigation. It is also important to understand farmers’ needs in terms

of seed supply, because it makes a large difference whether the farmer predominantly use their own seed (or the seed of their neighbours), or usually buy seed from the formal sector.

9.4.2 Identification of the target environment and users

Once the criteria are set, the actual process of identification needs the involvement of partners who have a very good knowledge of both the environment and the users. These are typically the staff of the extension service or the staff of the outlying research stations. The first step is to set meetings with all the stakeholders with the objective of identifying partners and locations.

In this phase there are some potential biases that can affect the success of PPB. Key decisions affecting the participatory programme are (i) whether to seek individual or group participation; (ii) whether the participants should be experts (germplasm experts are farmers who regularly experiment with varieties, are able to recognize important intra- as well as inter-varietal differences, and who target specific varieties to different micro-niches) or whether they should represent the wider community; and (iii) whether equity should be the main objective in the identification of the users. Meetings with all different typologies of farmers may be inappropriate without a proper knowledge of the power relationships within the community. This usually leads to a few farmers monopolizing all the discussions reducing the possibilities for others to express their views. This danger varies greatly with the culture: in some cultures, women are not even allowed to attend meetings; in others, they can participate with a passive role; and in others they can participate freely and with the same rights as the men. Therefore, it is not possible to give a 'cookbook formula' for what works better. In general, if some groups or individuals tend to be discriminated against, it may be appropriate to have separate meetings with different social, gender, age or wealth groups.

In the process of identifications of users, it is very important to clarify (i) what plant breeding can offer and how long it can take; (ii) what sort of commitment in land, time and labour is required from the farmer; (iii) what is the risk for the farmer and how this can be compensated for (in-kind compensation vs. money), and (iv) what the overall benefits are that the farmers can expect if everything goes well.

In these meetings it is also essential to understand what sources of seed farmers use for the various crops, to anticipate which type of change the participatory programme might introduce, and to make sure that farmers are aware and prepared to absorb the changes.

The organizational issues of the choice of sites are both at the macro- (identification of villages or locations within a country or a region) and at the micro-level (identification of the field within a village for planting the trial(s). The participation of farmers in the identification of the fields is unavoidable because it is associated with the relevance of the results and with the issues of 'who participates' and 'who benefits': it is at this point that small-scale farmers run the risk of being excluded as active participants because their land is not large enough to host trials in addition to the farmers' crop. As we will see later, it is possible to find experimental designs that allow distributing relatively large number of entries in small blocks, each planted in a different farmers' field.

An additional organizational issue in the choice of the sites, which is associated with the issue of the breeding philosophy, is whether they should be sufficiently representative to allow some degree of extrapolation of the results to other sites, or whether the priority should be to meet farmers' needs to target micro-niches. In practice, it is advisable that sites do represent the range of environmental and agronomic conditions in which the crop is grown, because this is known to have a major effect on farmers' selection (Ceccarelli *et al*., 2000, 2003).

Participatory breeding programmes are often seen exclusively as programmes leading to niche varieties, adapted to only a restricted complex of environmental and social characteristics (see also Chapter 4). This is not necessarily true, as the type of adaptation (narrow or wide) of the varieties emerging from a PPB programme is largely dependent upon the nature of the locations and the users. If the locations covered by the programme represent a mix of favourable and unfavourable growing conditions, it may be expected that the more uniform environmental conditions that generally characterize favourable environments will led to the selection of the same varieties across a number of locations (widely adapted in a geographical sense), assuming that farmers' preferences are also homogenous across the same locations. In the more unfavourable conditions, one can expect that more location-specific varieties (narrowly adapted) will be selected. Eventually, even if the selection is conducted independently in each of many locations, giving the impression that selection is for specific adaptation, the process will not discard a truly widely adapted genotype if such a genotype does exist in the breeding material (Ceccarelli, 1989). Therefore a PPB programme easily results in a mixture of widely and narrowly adapted varieties.

What is discussed above also depends on the definition of wide and narrow adaptation. Narrow and wide are relative terms; therefore, for an international breeding programme, a widely adapted variety is a variety performing well in a number of countries, while for a national breeding programme it is a variety performing well in several locations within the country, while, ultimately, to a farmers it means a variety performing well across cropping seasons – without too much concern whether it performs well elsewhere.

It is difficult to reach an optimal allocation of resources regarding to the number of sites and to the number of farmers at each site. As we will see later, it is possible to organize a PPB programme in such a way that G×E interaction, and more specifically Genotype × Location (G×L) and Genotype × Years within Locations (G×Y(L)) will eventually optimize the overall structure, at least from a biological point of view. This aspect is covered in depth in Chapter 20.

9.4.3 Type of participation

Several scientists (Biggs and Farrington, 1991; Pretty, 1994; Lilja and Ashby, 1999a, b; Ashby and Lilja, 2004) discriminate among different types or modes of participation, which are not necessarily mutually exclusive, although there may be trade-offs among the impacts of the different types. Based on two groups of decision-makers, namely 'scientists', which includes research programmes and extension agencies, and 'farmers', which refers to the intended users of the participatory breeding programme varieties, PPB is categorized by Ashby and Lilja (2004) as:

- ***Consultative*** Scientists make the decisions alone, but with organized communication with farmers. Decisions are not made with farmers nor delegated to them.
- ***Collaborative*** Decision-making authority is shared between farmers and scientists

based on organized communication between the two groups. Scientists and farmers know about each other's ideas, hypotheses and priorities for the research through organized two-way communication. Plant breeding decisions are made jointly; neither scientists nor farmers make them on their own. Neither party has the right to revoke or override the joint decision.

- ***Collegial*** Farmers make plant breeding decisions collectively, either in a group process or through individual farmers with organized communication with scientists. Farmers know about scientists' priorities and research hypotheses through organized one-way communication. Farmers may or may not let this information influence their plant breeding decisions.

Ashby and Lilja (2004) also recognized *Conventional* (no farmer participation) and *Farmer experimentation* (no scientist participation; most of the pre-1900 breeding was of this type) as two additional typologies of PPB. In the first, scientists make the decisions alone without organized communication with farmers, while in the second, farmers make all the decisions, either as a group or as individuals, on how to experiment, introducing new genetic material without organized communication with scientists.

We will not discuss these last two typologies any further, because they represent two types of plant breeding that explicitly exclude participation of either one or the other of the two essential partners.

Two other two categories of PPB were defined by the Plant Breeding Working Group (PBWG) of the System-Wide Programme for Participatory Research and Gender Analysis (SWPPRGA), and by McGuire, Manicad and Sperling (1999), Weltzien *et al.*, (2000, 2003) as *Formal-Led PPB* when farmers join in breeding programmes which have been initiated by formal breeding programmes, and as *Farmer-Led PPB* when scientists seek to support farmer's own systems of breeding, variety selection and seed maintenance.

In practice, field experience indicates that PPB is a continuously evolving process. It is quite common that, as farmers become progressively more empowered—an almost inevitable consequence of a truly participatory breeding programme—a consultative programme gradually evolves into collaborative and collegial. Similarly, a Formal-Led PPB can gradually evolve into Farmer-Led PPB, and could eventually be entirely handed over to farmers.

9.4.4 Choice of parental material

The choice of parental material is of critical importance in a breeding programme and in this book is covered in Chapters 3 and 6. Here we only add that, as in a conventional breeding programme, the parental material in a participatory breeding programme is, with few exceptions, the best material selected, by farmers in the case of PPB, in the previous cycle.

9.4.5 Choice of breeding method

The breeding method is only one of the factors determining the success of a breeding programme; the others include the identification of objectives and the choice of suitable germplasm (Schnell, 1982).

In conventional breeding programmes, the choice of the breeding method is purely the responsibility of the breeder and is largely affected by the breeder's scientific background and by the mandate of the organization, public or private, for which the breeder works.

In PPB, the choice of the breeding methods can not be made without considering whether and how farmers are handling genetic diversity. The rationale is as follows. As described in Chapter 3, the generation of variability is the first step of any breeding programme, conventional or participatory, followed by the utilization of variability and eventually the testing of the prospective varieties. In a number of countries, farmers do use genetic diversity either as a specialized activity within the community, or as an individual initiative (Chapter 22).

For example, in Eritrea it is common for farmers to select individual heads within a wheat or a barley plot, plant them as head rows in a small portion of their field, decide whether to bulk one or more rows and start testing the bulk in the field of other farmers, initially on a small scale and gradually on a larger area. One of the most widely grown wheat varieties in the country has been developed starting from a small seed sample bought by an expert farmer in a local seed market and planted initially as spaced plants. In Nepal, before harvesting the crop, farmers growing the old barley landraces habitually collected a sample of heads representing all the different morphological types present in the field to produce the seed to be planted in the following cropping season. In contrast, in the Syrian Arab Republic and in many other countries in the Near East and North Africa, the selection unit is a plot, and excessive heterogeneity within a plot not only is not exploited, but is also considered undesirable.

These three examples indicate that, even within the same crop, a participatory breeding programme has to use different breeding methods, at least at the beginning of the programme, to ensure full participation. It is obvious that a blanket approach, based on the same breeding method used everywhere regardless of whether and which skills farmers have in handling genetic variation, can not ensure true participation, as farmers will be confronted with methodologies they can not relate to anything with which they are familiar.

In addition to the examples given earlier, breeding methods may differ for the same crop within the same country. Using Africa as an example, barley is grown in Ethiopia and Eritrea both as food and feed (largely landraces) and also for malt production for local breweries. While population methods can well be used in the first case, pedigree breeding is suitable in the second.

An issue related with the choice of the breeding method is how much breeding material farmers can handle. This is a controversial issue, and several scientists believe that farmers can only handle a very limited number of genotypes and therefore, implicitly, believe that the only form of participation is PVS. If true, this will make it impossible to implement true PPB programmes, because plant breeding needs to start from a sufficiently large sample of genetically variable material.

Field experience shows that when discussing the number of genotypes farmers can handle, it is very dangerous to make assumptions before discussing the issue with the farmers.

The choice of the breeding method also depends of the genetic structure of the final product, i.e. pure lines, mixtures, hybrids or open pollinated varieties. It is important to note that farmers can change the type of final product originally planned by the breeder. For example, in Syria, where, in the case of self pollinated crops, the formal system only accepts pure lines for release, farmers do not mind adopting bulks as long as they are not too heterogeneous. In the case of barley, we also have the example of one farmer testing the advantage of a mixture of a 6-row genotype, adapted to high rainfall and lodging resistant, with a 2-row genotype adapted to low rainfall and lodging susceptible. Similarly in Egypt, we found that farmers plant a mixture of all the lines selected one year earlier (Grando, pers. comm.).

In principle, all breeding methods can be employed in PPB, keeping in mind that 'participatory' does not mean that ALL the breeding material has to be planted in farmers' fields. Several examples of different breeding methods used in actual participatory breeding programmes can be found in Almekinders and Hardon (2006).

Given that plant breeding is a cyclic process (see Figure 9.2), one organizational issue that is often debated is the stage of the plant breeding programme at which participation should start. This issue in effect makes the difference between PPB and participatory variety selection (PVS; see Chapter 3, section 3.7), where the participation of farmers takes place during the third stage of the breeding process, after the genetic variability available at the beginning of the cycle has been—usually—drastically reduced. We believe that farmer participation should, at a minimum, coincide with the second stage of a breeding programme, possibly when the genetic variability is still at or near its maximum. There are examples of PPB programmes where farmers can start as early as making crosses, such as the PPB rice programmes in Bhutan and Viet Nam (SEARICE, 2003), which does not necessarily imply emasculation and manual pollination, but, for example, mixing different genotypes or cultivars of cross-pollinated crops to facilitate intercrossing. Even when they do not manually make the crosses, in a PPB programme that runs over cycles of selection and recombination like any other plant breeding programme, farmers control the crossing programme by selecting the best entries, which are usually the parents of the following cycle, as discussed earlier under choice of parental material.

Eventually, a breeder planning to start a PPB programme is faced with the issue of whether the breeding method used in a non-participatory programme needs to be changed. While there are breeding methods that are easier to fit into a participatory context, a breeder does not have necessarily to change the breeding method, given what was said earlier about fitting the method to whatever type of breeding farmers are already doing. Here, we might add that, like other aspects of PPB, the methodology can also evolve as new farmer skills emerge. Several examples can be found in Almekinders and Hardon (2006).

9.4.6 Management of trials in farmers' fields

The organizational issues of implementing trials in farmers' fields differ considerably from those in a research station, and are more similar to those of a DBP. However, they diverge significantly from a DBP when farmers take full responsibility for planting and harvesting.

The first differences are issues such the choice of the actual portion of land on which to plant the trial, the total number of plots in each trial, the type of controls (check varieties), the plot size, the seed rate, the distance between rows, the dates of planting and harvesting: all these have to be discussed with each community in each location. It is not simply a matter of courtesy. Farmers' interest in the trial is directly proportional to their participation in its design and management. The inability of the scientists to accommodate farmers' requirements may lead to a total lack of interest by the farmers. For example, in the case of barley in the Syrian Arab Republic, farmers believe that seed rate is extremely important. Whether this belief is correct or not is immaterial, because if the scientists use the seed rate they believe right, farmers may even refuse to carry on selection. Therefore, in the participatory barley breeding programme in the Syrian Arab Republic, for example, we are using as many as eight different seed rates, ranging from 50 kg/ha to 250 kg/ha. As this is believed by the farmers to have a major effect on barley yields, an important side-activity would be the visits of farmers to locations where a very different seed rate is used; this might be the best way to generate an interest in testing alternative seed rates.

One fundamental principle in discussing organizational issues with farmers' communities is to pose and justify the problem, not to present a solution. The solution should come from the community, and if the community or the individual farmers are not prepared to solve the problem, a possible solution can be offered, but only as a suggestion.

The choice of land, which in a CBP usually depends on the farm manager, in the case of a DBP (whether participatory or not) has to be agreed on by the farmer. It has to represent a suitable rotation and a good uniformity (this should be checked the year before, together with the past history of the field). The size required by the trial may not match that allocated by the farmer to that specific rotation. In this case, the extra land has to be planted by the scientists with a cover crop using a variety chosen by the farmer.

The type of genetic material to be used in the programme needs to be discussed with farmers. Initially, the scientists may find that farmers are not aware of the diversity within the crop, and in this case our suggestion is to start with a wide array of genotypes representing as wide range of diversity as possible. But there are cases where farmers have previous experience with various type of germplasm and they may feel very strongly concerning one or more types of specific germplasm type. For example, in he Syrian Arab Republic, farmers grow two landraces: one with black seed, which is grown predominantly in dry areas, and one with white seed, which is grown predominantly in wetter areas. Farmers feel very strongly about the seed colour and therefore in the participatory barley breeding programme in the Syrian Arab Republic we make available different initial genetic material in the two areas. The issue of the type of genetic material covers also the issue of the checks. The checks have the dual purpose of providing an estimate of error variance (for example, in unreplicated trials with systematic checks) and to provide a comparison for farmers during selection. The ideal solution is to have a well adapted variety to fit both purposes, and if the choice of the check(s) is left, as it should be, to the farmers, this is usually their choice.

The issue of managing the equipment in a PPB programme is similar to a DBP. If the country has a network of research stations each with its own equipment, it is obviously more economical that each station uses its own equipment for all the field operations. Where machinery has to be moved from one central research station to all the trials sites, the number of sites and of trials has to be adjusted to allow all the necessary operations to be performed in time. Usually farmers are extremely concerned about planting and harvesting at the right time, and if the choice is between having several locations and being late in both planting and harvesting in some of them, it is advisable to reduce them to a number that can be managed properly. The issue of timely harvesting, in the case of completely mechanized crops, can be solved by estimating yield through a hand-harvested sample of the plots. This has the additional advantage of estimating the total biological yield, a character of major importance in many developing countries. The farmers can then harvest by combine whatever is left in the field. This of course assumes that the seed requirements for the following year are satisfied. The need for timely planting and harvesting makes it much easier to organize a PPB programme in countries or for crops where both planting and harvesting is done by hand. In this case, the scientists can limit themselves to the preparation of the trials, visit each site to show the trial layout, leave the envelopes or the bags properly numbered, and let the farmers do the planting themselves, as it happens in a PPB programme for barley in Iran.

The issue of managing the equipment in a situation of fully mechanized operations can also be addresses by empowering farmers to conduct trials. This often poses technical challenges, because commercial drills and combines are not suitable for planting experimental plots.

Finally, two additional issues in managing trials in farmers fields concern the physical layout of the trials, and the management of crop residues, border rows and leftovers (in the case of sampling).

In arranging the trials on the ground, two principles are important: the first is that no land should be left uncultivated. In many farming communities in developing countries, leaving even a few square metres of land uncultivated is considered almost a crime, and this is particularly true in marginal and dry areas where yield per unit of land is low. Therefore, no gaps should be left between plots, as is common practice on research stations to facilitate the identification of plots, and the alleys should also be planted. To facilitate farmers during selection, and to avoid seed mixture if the seed from the trial is to be used the following year, the first and last rows of the plot can be harvested by hand shortly before selection and harvesting. Similarly, the alleys can be mechanically slashed or hand harvested to facilitate moving across the field and harvesting. The second principle is to lay out the trial in a fashion that it occupies a piece of land of regular shape, because this facilitates the handling of the rest of the land by the farmer.

The management of trials residues (borders, fillers around trials, border rows and what is left of a plot after taking samples) is an important organizational issue because it is a potential source of dispute. As a general principle, as in many other organizational issues in PPB, this needs to be discussed in advance with farmers, justifying why the handling of experimental plots is different from the handling of a field planted for large-scale production, underlining the need to generate information to use later in selection, and the need for as much precision and accuracy as possible to obtain correct estimates of the genotypic values of the breeding material (the scientists do not necessarily have to use these terms when discussing with farmers!). As mentioned earlier, the guiding principle is to justify and pose the problem, and involve farmers in the process of finding the most mutually suitable solution.

9.4.7 Farmer selection

An organizational issue peculiar to participatory breeding programmes is the selection done by the farmers. This is one of the most important operations (and one that makes the breeding programme participatory). It is also one of the activities that, if done properly, can generate a strong sense of ownership, and enhance farmer skills as far as knowledge of the genetic material is concerned.

As for other organizational issues, it is impossible to give general recommendations, because the baseline can be very different in different communities. One of the extreme situations is represented by communities where there is only a vague notion that different varieties do exist, but farmers have had only sporadic contacts with scientists, and these contacts have been mostly of the type "I am here to tell you what do; you do it, and I will come back to check if you did it well!". In these communities, farmers often ignore the sexual reproduction in plants and therefore the diversity itself within a crop is surrounded by an aura of mystery. The other extreme is represented by communities who already have a solid experience in breeding and experimenting.

Most of our experience has been with the first type of situation, which is not necessarily the most difficult, but is certainly the one in which PPB takes more time to develop and one in which PPB evolves from consultative to collegial (as defined under 9.4.3). Therefore we will illustrate some general principles that we followed with the first type of situation, and how these principles need to be modified in the case of the second situation. We will consider in particular two aspects of farmers selection, namely 'when to select' and 'how to select'.

The timing of selection depends strongly on the crop and its uses, on the environment and on the traits farmers consider important. This is a typical aspect of the overall activity, and one which needs to be discussed with farmers during the planning of the programme because it has implications for the amount of time farmers need to allocate to selection and on the total number of experimental units (plots or plants) farmers can handle. It also has implications for the degree of involvement of the scientists where some of the traits that are important to the farmers need to be measured.

The choice of the ideal time for selection is highly individual: some farmers prefer to visit the field often during the cropping season, while others, particularly in unpredictable environments, claim that only shortly before harvesting is it possible to assess the real value of the breeding material. Farmers may also change their preferences in relation to both when and how to select. Farmers who were used to an organized 'selection day', whereby all the farmers assembled at a meeting point and visited and scored the various trials, subsequently demanded to do the selection by themselves on a date convenient to them. In fact, it is obvious that while the first way of organizing the selection favours exchange of ideas among the participants, it also implies fixing a date in advance that later may be no longer convenient to some participants. The second solution has the advantage of allowing many more farmers to do the selection as they are free to choose when to do it. This obviously requires that the scoring sheets be made available ahead of time.

The scoring method using by farmers during selection is another organizational issue, and like many others, the starting point can be different in different countries and in different communities within the same country. In some communities, some farmers are used to score different entities based on merit or value; in others there is no previous experience. The example of scoring school homework is often useful. For some farmers, it is easier to use words representing different categories such as ‘undesirable’, ‘acceptable’, ‘good’, ‘very good’ and ‘excellent’, which later be translated into a numerical scale. With time, and particularly with those farmers participating regularly in the selection session(s), the scoring method may change, particularly when farmers within the same community use different methods, and farmers will eventually converge towards a common scoring method.

When scoring implies ‘writing’ (words, symbols or numbers) there is risk of excluding farmers unable to read or write. The problem can be solved by flanking the farmers who need assistance with a researcher, an extension staff member or another farmer; this requires additional organizational arrangements, particularly in remote areas. In those cases, the ideal solution is to make the communities capable of organizing themselves as much as possible.

Other methods of scoring breeding material include the identifications of the best entries with ribbons of different colours (depending on the category).

9.4.8 Visits to farmers

In a participatory breeding programme it is very important to maintain contacts with farmers beyond and besides specific scientific activities. These ‘courtesy‘ visits are not only instrumental in building and maintain good human relationships between scientists and farmers by bridging gaps, but are an incredibly fertile reciprocal source of information. Often farmers like to converse on issues not directly related with the specific participatory programme, but related to the multitude of challenges that farmers, particularly those in marginal agricultural environments, continually face. This helps scientists to put the issue of developing new varieties of a given crop in a broader context.

9.4.9 Note taking, data management and analysis

The trials conducted in a participatory breeding programme need to generate the same quantity of information and of the same quality as those in a conventional programme, for two reasons: first, because the information has to be used to take the final decision of which material to promote and which material to discard, and, second, because the information can be later used in the phase of variety release. We learned that in addition to the visual selection, farmers may want to have access to some quantitative data to reach a final decision. This is an additional issue to discuss at the onset of the programme because if this is required by the farmers, the trials have to be organized in such a way as to allow collecting data on the traits considered important by farmers, analysing the results with appropriate statistical analysis, and reporting the results in a format that makes the information fully accessible to farmers.

Collecting field data may go beyond the time, the facilities and the expertise of the farmers, but this is a possibility that can not be ruled out *a priori*. However, as in most similar cases, the issue needs to be discussed with the farmers so that it is becoming almost a service that the scientists provide them.

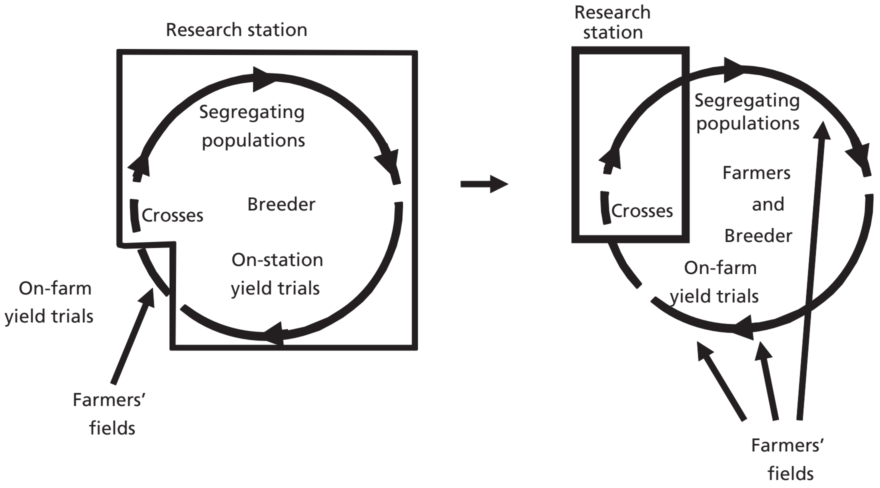
As for the analysis of data from participatory breeding trials, the reader could refer to Bellon and Reeves (2002), who present a wide range of analytical tools, and to Chapter 20 in this volume.

9.4.10 Managing the transition phase

In this section we will consider the organizational issues faced by breeders who decide to migrate from a CBP to a

FIGURE 9.2

Conventional plant breeding is a cyclic process that takes place largely within one or more research stations (left) with the breeder taking all decisions; participatory plant breeding is the same process, but takes place mostly in farmers' fields (right) and the decisions are taken jointly by farmers and breeders



decentralized and participatory breeding programme. We will not consider the case of transforming a decentralized non-participatory breeding programmes into a participatory programme because this only require solving the organizational issues associated with farmer participation.

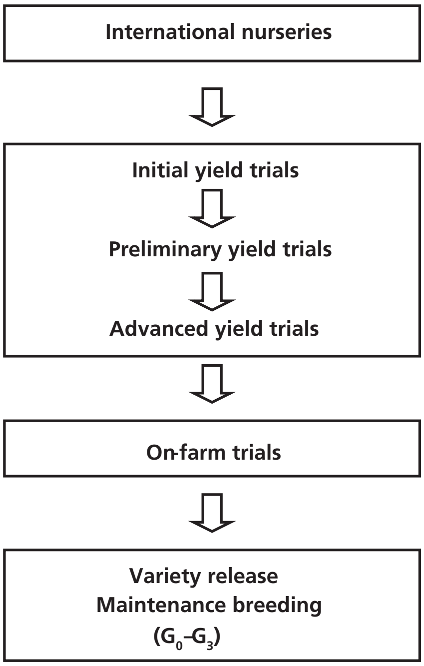
In general, the problem is to transfer a cyclic process taking place largely within one or more research stations (Figure 9.2, left) to farmers' fields (Figure 9.2, right), and to change the process of decision-making in the way discussed earlier. The general organizational issues in managing the change is that, because it is unwise to get rid of breeding material, the transfer of the programme to farmers' fields should start from the first step that the breeder intends to transfer and implies that, till the transfer is completed, the CBP and the DPBP will coexist. This should be clearer from the examples given later.

We will discuss two scenarios, which are the most common in breeding programmes in developing countries. The first scenario concerns breeding programmes that do not generate genetic variability, but in which the base germplasm is introduced from other institutions (generally international breeding programmes) and sometimes include locally collected germplasm and wild relatives. The second scenario is fully-fledged breeding programmes with all the steps described in Chapter 3, and which may include acquisition through germplasm collection and molecular breeding.

First scenario: breeding programmes with only the selection and testing stages

We will examine the organizational issues in managing the transition of a plant breeding such as the one shown in Figure 9.3, which represents a situation common to several countries. In such a breeding programme,

FIGURE 9.3
Schematic representation of conventional plant breeding that relies on introduced breeding material as the source of genetic variability



All the phases before the on-farm trials are conducted on a research station.

the first step (as defined in Chapter 3) is replaced or represented by the introduction of breeding material (including segregating populations, nurseries and yield trials) from other breeding programmes, usually from international organizations. The incoming breeding material is grown on station for an initial cycle of selection (mostly negative selection), followed by a series of yield trials conducted in a number of research stations for a number of years. The yield trials have different names (we will use initial, preliminary and advanced), and most typically are conducted over a period of three or more years: during this period the number of entries decreases and the plot size increases.

At the end of the three or more years of on-station testing, the entries considered as promising are tested in on-farm trials, which are usually repeated for two or three years and generate the data used, together with those obtained on station, to support the submission of a variety for release. There are cases in which the on-farm trials, or at least some of them, are also conducted on station.

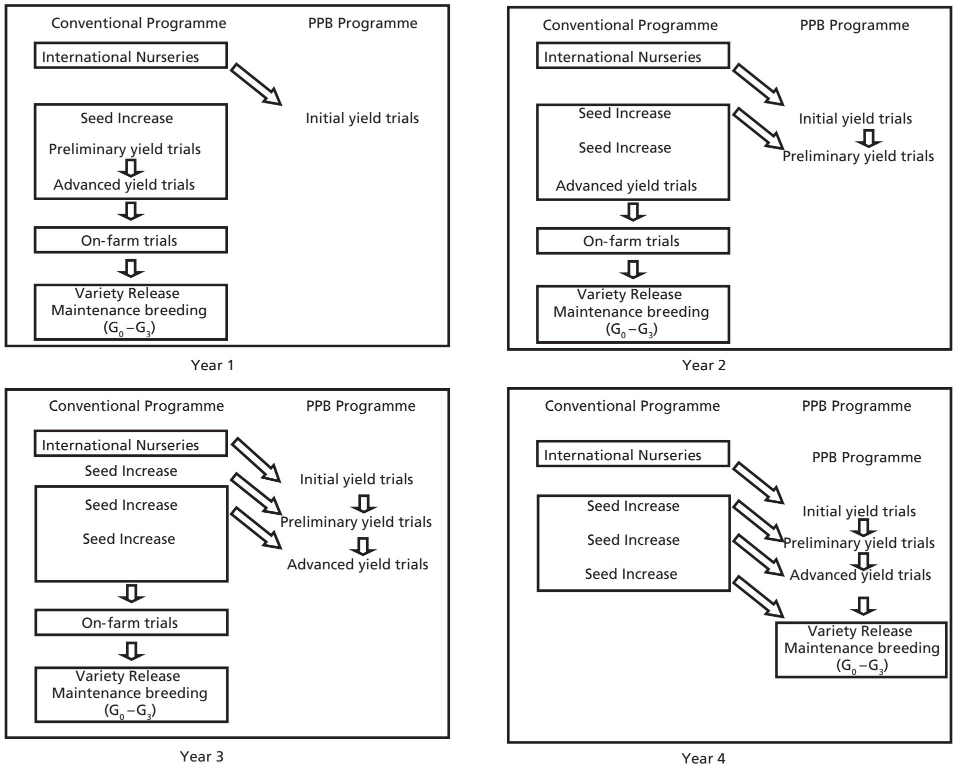
The possible steps to modify such a programme are shown, year by year, in Figure 9.4. The process of modification begins with planting the initial yield trials in farmer's fields (where and how many is based on what has been discussed earlier in this chapter) rather than on station. Therefore, in the first year of the participatory programme, all the nurseries and trials will be as in the conventional system, except the initial yield trials, which will be planted in farmers' fields. The remnant seed of the initial yield trials is planted in a research station with reliable rainfall or irrigation facilities for seed increase.

In the second year, the preliminary yield trials, containing the entries selected by the farmers in the various locations, will be planted at the same sites using the seed produced on station. Using a common seed source is important to avoid biased comparisons between entries selected in different locations. Also, a new set of initial yield trials will be planted in farmer's fields. On station, together with the advanced yield trials of the conventional programme, the seed increase of the breeding material tested in both the initial and the preliminary yield trials will be conducted.

In the third year, the advanced yield trials, containing the entries selected in the preliminary yield trials by the farmers in the various locations, will be planted at the same sites using the seed produced on

FIGURE 9.4

Steps to modify a conventional plant breeding programme that relies on introduced breeding material as the source of genetic variability into a decentralized-participatory breeding programme



In each box the conventional program is on the left and the participatory on the right

station; therefore, in the third year, all the three categories of trials will have migrated into the PPB programme, while only seed multiplication is conducted on station.

In the fourth year there is no more need to plant the 'on-farm trials' because all the trials have already been conducted on farm, and if the data are considered sufficient, and there is material worth releasing, the procedure for variety release can be initiated, while the promising lines are further multiplied.

A number of activities can be conducted on station in parallel with the participatory programme. For example, the incoming breeding material can be tested for important pests and diseases, while multiplying the seed for the initial yield trials, as the screening can continue in suitable locations (plastic houses, hot-spot sites) during all testing and selection stages, using part of the seed kept for increases.

Also, the lines from the advanced yield trials that are candidates for release can be used as parent in a crossing programme. As we are discussing the case of a breeding programme without crossing programme, these lines could be sent to the institution(s) supplying the incoming breeding material with a request that they use them in targeted crosses. Incidentally, this is a case of PPB in which the partners are two breeding programmes, one national and one international.

Links can be also easily established with the activities of one or more genebanks, where they exists For example, a genebank could conduct a preliminary evaluation of new germplasm (locally collected or acquired from other genebanks), involving farmers in the assessment. The selected accessions, after one further cycle of seed multiplication, can then pass into the PPB programme in the initial yield trials. The information collected on the material coming from the genebank should be shared with the genebank, becoming part of the Passport data.

Second scenario: fully-fledged breeding programmes (self-pollinated crops)

The migration of a fully-fledged CBP is more difficult to generalize because of the multitude of methods used to handle the segregating populations, even within crops characterized by the same mating system. Therefore, we will examine the case of some of the most commonly used breeding methods, illustrating how they can be changed into a participatory programme.

Figure 9.5 illustrates a typical example of a breeding programme of a self-pollinated crop, based on a classic pedigree method. This is still fairly widespread in several developed countries, and can be easily transformed into a participatory programme, by moving the on-station yield

FIGURE 9.5

Schematic representation of a conventional plant breeding programme of a self-pollinated crop based on a classical pedigree method (left): all the phases before the On-farm Verification trials are conducted on research station. On the right, the same programme conducted in a participatory mode

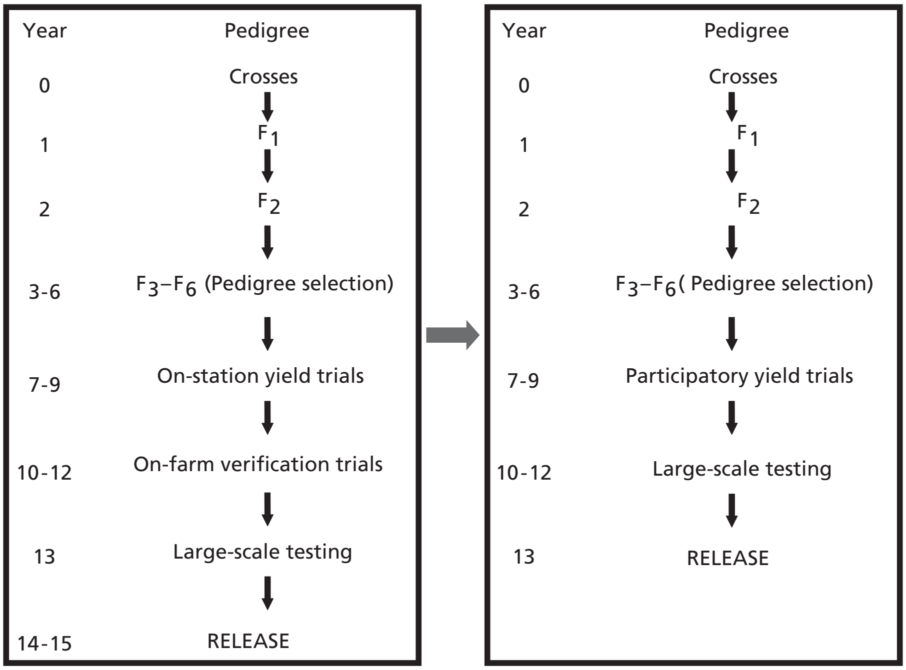
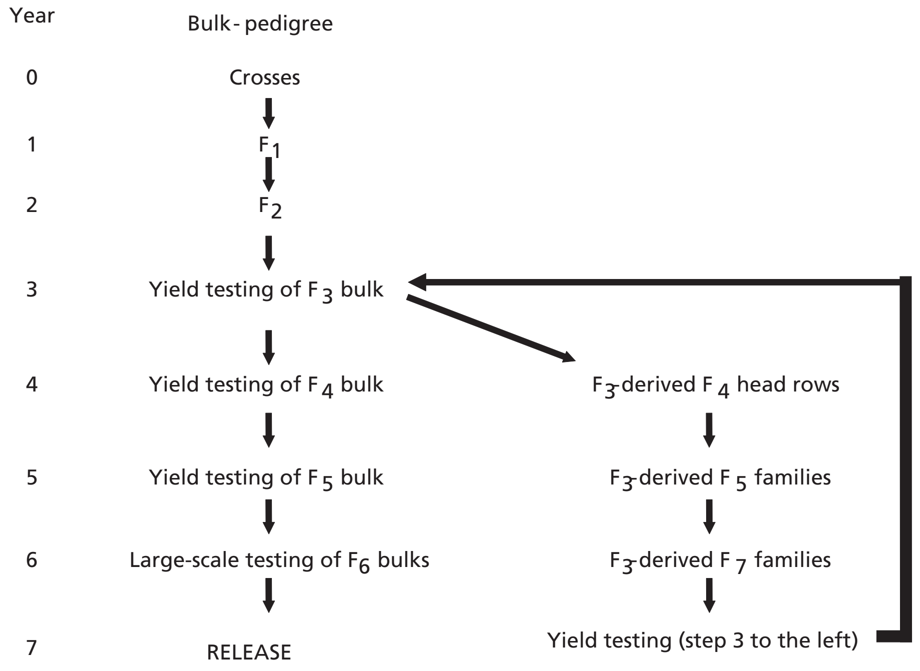


FIGURE 9.6

Schematic representation of a participatory plant breeding programme of a self-pollinated crop based on a bulk-pedigree method that allows selection between crosses in farmers' fields through yield testing in three successive cropping seasons (left) and selection within selected crosses on station (right)



The pure lines derived from selection within populations will be yield tested through steps 3 to 6.

trials onto farmers' fields in a phased fashion, as shown in Figure 9.4. This will make the 'on-farm verification trials' redundant, so that the change will shorten the period before release by at least three years, and the choice of the candidates for release can be based on farmers' preferences rather than on agronomic performance alone.

The migration from the classical on-station pedigree method on the left of Figure 9.5 to the equivalent programme conducted in a participatory mode (Figure 9.5, right) takes place through the steps shown in Figure 9.4.

One alternative breeding method that allows selection, both between and within crosses, to be conducted in a participatory mode is the bulk-pedigree method shown in Figure 9.6.

The method, described in detail by Ceccarelli and Grando (2007), is based on the yield testing in farmers' fields of early segregating populations (F_3 bulks). The selected bulks are yield tested as F_4 bulks for a second year, and those that are selected are tested for a third year as F_5 bulks. In parallel to the yield testing of the populations (selection within crosses), it is possible to conduct on-station pure-line selection within the selected populations (left) by collecting heads of the selected F_3 bulks. The F_3-derived F_4 head rows are promoted to the F_5 only if farmers select the corresponding F_4 bulks. The process is repeated in the F_5 and the resulting families, after one generation of increase, return as F_7 in the yield-testing phase. Therefore, when the model is fully implemented, the breeding material that is yield tested includes new bulks as well as pure lines extracted from the best bulks of the previous cycle.

The method has a number of advantages: (i) the participation of farmers can be introduced very early in the overall process. The method can actually start with the F_2 if the amount of seed available is sufficient; (ii) during the pure-line selection, it is possible to screen for biotic stresses, quality traits or other traits important to farmers and with high heritability, using conventional or molecular approaches; and (iii) the method can also be used solely for selection between crosses in those cases where the system of variety release is not too strict in terms of uniformity.

While the aspects of managing the transition phase have been discussed with specific reference to self-pollinated crops, the concepts underlying the process are equally applicable to cross-pollinated crops.

9.4.11 Institutionalization of participatory plant breeding

Institutionalizing PPB (i.e. mainstreaming and scaling-up) must be one of the main objectives when setting up a participatory breeding programme. This is because it is very unlikely that individual, small-scale PPB projects, even though very successful at local level, will ever determine impact at national level in terms of production increase, for example, even if this is not the only impact expected from a PPB programme. At the same time, only collaboration between the institutions that have responsibility for plant breeding and farmers could exploit the relative advantages of the two partners, i.e. the extraordinary ability of institutions to generate variability, and their continuity, versus the extraordinary ability of farmers to extract what can improve their livelihood from that variability under their conditions.

We have already given an example of the technical aspects of institutionalizing in the section *Managing the transition phase*. However, the major issue with the institutionalization of PPB is to make this method acceptable to national and international research institutes as being the way in which plant breeding is conducted by the institute.

Unfortunately, the several cases of both successful and unsuccessful institutionalization of PPB do not allow drawing a general lesson or a general methodology on how to obtain institutional recognition of PPB as an approach that effectively combines the development of improved varieties with development objectives aiming at alleviating rural poverty and improving local food production (Almekinders and Hardon, 2006).

One good example to illustrate how difficult it is to understand what influences policy and managers of agricultural research is the experience at ICARDA based on the work done in nine countries (Algeria, Egypt, Eritrea, Iran, Jordan, Morocco, the Syrian Arab Republic, Tunisia and Yemen) with a number of crops, with one in common (barley), by the same team of scientists with a similar methodology. This work yielded contrasting results in terms of institutionalization, ranging from institutional rejection, as in the Syrian Arab Republic and Egypt, where the programme continues as a direct ICARDA-farmers collaboration, and Tunisia, where, at the end of a special project, all the activities ended, to full insti-

TABLE 9.1

Status of nine PPB programmes conducted by the same Institution (ICARDA) in nine different countries and date of Institutionalization

Country	Crop(s)	Date started	Date ended	Date of institutionalization
Syrian Arab Republic	B	1995/96	Continuing	N/A
Morocco	B	1996/97	Continuing	2000 (see text)
Tunisia	B	1996/97	1999	N/A
Yemen	B, L	1999	2002	2003 (see text)
Jordan	B, C, BW, DW	2000	Continuing	2005
Egypt	B	2006	Continuing	N/A
Eritrea	B, L, C, F, BW, DW	1998	Continuing	1998 (see text)
Algeria	B, DW	2006	Continuing	2007
Iran	B, BW	2007	Continuing	2008 (see text)

Key to crops: B= barley; L = lentil, C = chickpea, F = faba bean, DW = durum wheat, BW = bread wheat.
Date is that at which the programme was fully supported by Government institutions either financially or ideologically (see text for details). N/A indicates not institutionalized.

tutional acceptance of the methodology, as in Algeria, Eritrea, Iran, Jordan, Morocco and Yemen even though with different timing and modality (Table 9.1).

In the Syrian Arab Republic and Egypt, national institutions were actually involved, but in the case of Syria, the collaboration was terminated, and in the case of Egypt, the institution involved is not the one having the mandate for plant breeding.

An intermediate institutionalization was observed in Morocco, where the National Barley Breeding Programme at INRA at the end of a project (the same project involving Tunisia) adopted PPB in the programme for dry areas only.

In Yemen, a two-year project has had the power of introducing the concept of participation in all the research activities of the institution (AREA), while in Jordan only the breeding programmes have been gradually transformed by NCARE into PPB programmes (the transformation is still in progress). In Jordan, as well as in Algeria, PPB is now taught at the Universities by the same national scientists who are implementing the programme in the field.

Eritrea and Iran are special cases. Eritrea, being a recently independent country, did not have an existing research programme, and therefore when ICARDA started its collaboration with the country, it was with participatory methodology involving both the Ministry of Agriculture and the University. In Iran, in contrast, one of the two leading institutions (DARI) involved in plant breeding was in favour of experimenting with PPB, while the other (SPII) was opposed. Therefore, in the area for which SPII is responsible, the current programme is conducted as an NGO-Farmers-ICARDA collaboration, with germplasm provided by ICARDA, while in the area for which DARI is responsible we have full institutional support, with provision of germplasm and latterly with full financial support of the programme by the Provincial Agricultural Office.

The different reactions of the Institutions are not easy to explain. For example, in the Syrian Arab Republic, after nearly 15 years during which we conducted travelling workshops for policy-makers (including members of the variety release committee), research managers and scientists, several training courses for scientists, the publication of two scientific papers in refereed journals with national scientists as co-authors, several seminars and university lectures, and more importantly the adoption by farmers of a number of varieties (not even considered for release) with large production increases, there is still institutional opposition to even consider PPB as a complementary approach to conventional breeding.

In contrast, and after only two years and with no travelling workshop, no training, no scientific papers, and only a few seminars and meetings, there has been a complete uptake of the methodology by at least one institution in Iran and a very similar reaction was observed from the two leading institutions in Algeria (INRA and ITGC) after only three years.

The facts that one crop is common to all cases, that in those countries with contrasting institutional reactions the crop is used mostly as animal feed, and that the farmers belong to the same culture, make it even more difficult to interpret the different attitudes of policy-makers and scientists.

It appears as if ultimately the success in institutionalizing PPB depends on individuals, on their attitude to innovations and on the power relationships within the institution. In our experience, the institutionalization has been enormously facilitated by the presence of a person within an institution with sufficient moral authority to influence all the others.

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REFERENCES

Almekinders, C. & Hardon, J., eds. 2006. Bringing farmers back into breeding. Experiences with participatory plant breeding and challenges for institutionalisation. Agromisa Special 5. Agromisa, Wageningen, Netherlands. 140 p.

Ashby, J.A. & Lilja, N. 2004. Participatory research: Does it work? Evidence from Participatory Plant Breeding. In *New directions for a diverse planet.* Proceeding of the 4th International Crop Science Congress, Brisbane, Queensland, Australia, 26 September–1 October 2004.

Atlin, G.N., McRae, K.B. & Lu, X. 2000. Genotype × region interaction for two-row barley yield in Canada. *Crop Science*, 40: 1–6.

Bellon, M.R. & Reeves, J. 2002. Quantitative analysis of data from participatory methods in plant breeding. Mexico, D.F., CIMMYT.

Biggs, S.D. & Farrington, J. 1991. Agricultural research and the rural poor: a review of social science analysis. Ottawa, International Development Research Centre (IDRC). 139 p.

Ceccarelli, S. 1989. Wide adaptation. How wide? *Euphytica*, 40: 197–205.

Ceccarelli, S. 1996. Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity. *In* M. Cooper & G.L. Hammers, eds. *Plant adaptation and crop improvement*, pp. 467–486. Wallingford, UK, CAB International; Andra Pradesh, India, ICRISAT; Manila, IRRI.

Ceccarelli, S., Grando, S., Tutwiler, R., Baha, J., Martini, A.M., Salahieh, H., Goodchild, A. & Michael, M. 2000. A methodological study on participatory barley breeding. I . Selection phase. *Euphytica,* 111: 91–104.

Ceccarelli, S., Grando, S., Singh, M., Michael, M., Shikho, A., Al Issa, M., Al Saleh, A., Kaleonjy, G., Al Ghanem, S.M., Al Hasan, A.L., Dalla, H., Basha, S., & Basha, T. 2003. A methodological study on participatory barley breeding. II. Response to selection. *Euphytica*, 133: 185–200.

Ceccarelli, S. & Grando, S. 2007. Decentralized-Participatory Plant Breeding: An example of demand-driven research. *Euphytica*, 155: 349–360.

Dodig, D., Zoric, M., Knezevic, D., King, S.R. & Surlan-Momirovic, G. 2008. Genotype × environment interaction for wheat yield in different drought stress conditions and agronomic traits suitable for selection. *Australian Journal of Agricultural Research*, 59: 536–545.

Falconer, D.S. 1952. The problem of environment and selection. *American Naturalist*, 86: 293–298.

Falconer, D.S. 1981. *Introduction to quantitative genetics*. 2nd ed. London, Longman Group.

Lilja, N. & Ashby, J.A. 1999a. Types of participatory research based on locus of decision making. Consultative Group on International Agricultural Research (CGIAR), Participatory Research and Gender Analysis (PRGA). PRGA Working Document No. 6.

Lilja, N. & Ashby, J.A. 1999b. *Types of gender analysis in natural resource management and plant breeding*. Consultative Group on International Agricultural Research (CGIAR), Participatory Research and Gender Analysis (PRGA). PRGA Working Document No. 8.

McGuire, S., Manicad, G. & Sperling, L. 1999. *Technical and institutional issues in participatory plant breeding done from the perspective of farmer plant breeding*. Working Paper No. 2. CGIAR System-Wide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Pretty, J. 1994. Alternative systems of inquiry for sustainable agriculture. *IDS Bulletin,* 25: 37–48.

Rizza, F., Badeck, F.W., Cattivelli, L., Lidestri, O., Di Fonzo, N. & Stanca, A.M. 2004. Use of a water stress index to identify barley genotypes adapted to rainfed and irrigated conditions. *Crop Science*, 44: 2127–2137.

Rosielle, A.A. & Hamblin, J. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Science,* 21: 943–946.

Schnell, F.W. 1982. A synoptic study of the methods and categories of plant breeding. *Zeitschrift für Pflanzenzüchtung*, 89: 1-18.

SEARICE. 2003. Strengthening farmers' agricultural diversity management systems. *In* CIPUPWARD. *Conservation and sustainable use of agricultural biodiversity: a sourcebook*, pp. 599–607. Los Baños, Philippines.

Simmonds, N.W. 1984. Decentralized selection. *Sugar Cane*, 6: 8-10.

Simmonds, N.W. 1991. Selection for local adaptation in a plant breeding programme. *Theoretical and Applied Genetics*, 82: 363–367.

Soleri, D., Cleveland, D.A., Smith, S.E., Ceccarelli, S., Grando, S., Rana, R.B., Rijal, D. & Labrada, H.R. 2002. Understanding farmers' knowledge as the basis for collaboration with plant breeders: methodological development and examples from ongoing research in Mexico, Syria, Cuba and Nepal. *In* D.A. Cleveland & D. Soleri, eds. *Farmers, scientists and plant breeding: integrating knowledge and practice*, pp. 19-60. Wallingford, UK, CABI.

Weltzien, E., Smith, M.E., Sperling, L. & Meitzner, L.S. 2000. *Technical and institutional issues in participatory plant breeding done from the perspective of formal plant breeding.* Working Paper No. 3. CGIAR Systemwide Programme on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation.

Weltzien, E., Smith, M.E., Meitzner, L.S. & Sperling, L. 2003. *Technical and institutional issues in participatory plant breeding - from the perspective of formal plant breeding. A global analysis of issues, results, and current experience.* PPB Monograph No. 1. PRGA Programme, Cali, Colombia.

CHAPTER 10

Selection methods. Part 2: Pedigree method

Flavio Capettini

10.1 INTRODUCTION

Since the beginnings of agriculture more than 10 000 years ago, crop producers have been striving to obtain better crops. Different procedures have been followed to reach their objectives, with various results. Modern plant breeders, after the re-discovery of Mendel's laws just over a century ago, tried to introduce new knowledge in the process, obtaining sizeable progress in a relatively short period of time. Although different formal methods have been described, there is the general impression that modifications are more the common rule in breeding programmes rather than the strict methods described in books. Ultimately, every applied breeder has their own approach and priorities to reach their objectives, using a package of breeding tools, available knowledge and resources. This package should be matched to the realities of their socio-physical environment, which include the mechanics of institute where the work is carried out, the crop, the agro-ecological target area, and the socio-economic parameters of the target farmer group. Besides all the above, resource availability is probably becoming more and more the most important factor in determining the size and methodology of a breeding programme, for both public and private entities. Obviously, revenue expectations also play a decisive role in the size of investment that is applied to a programme.

10.2 PEDIGREE METHOD

The Pedigree Method—or to be more precise: the Modified Pedigree Method—is probably the most popular protocol used by plant breeders to advance generations during the inbreeding process in self- and cross-pollinated species, aiming to obtain desirable homozygous lines. Although there are as many modifications as breeders available, the general principle is what gives the method its efficacy: the genetic value of an individual can only be proven by the performance of its offspring. This method relies strongly on the maintenance of records of the parent-progeny relationships. Selection is usually performed on visual (or laboratory, marker assisted selection (MAS), etc.) assessment of significant, highly heritable traits. Many reasons drive breeders to combine pedigree with mass or bulk methods (Table 10.1).

TABLE 10.1
Example of a programme following the Pedigree Method

Growing Cycle	Procedure
1	Plant 250 – 5000 F$_2$ plants. Select individual plants (300)
2	Grow F$_{2:3}$ rows (300) Select best rows (50) Select best plants in rows (2–3)
3	Grow F$_{3:4}$ lines (150) Select best families (25) Select best rows in families (3) Select best plants in rows (2)
4	Grow F$_{4:5}$ lines (80) Select best families (15) Select best rows in families (2–3) Select best plants in rows (1)
5	Grow F$_{5:6}$ lines (20) Select best families (15) Harvest best rows in bulk
6	Testing of F$_{5:7}$ lines in two locations, one rep per loc.
7	Multi-location testing begins (F$_{5:8}$). Harvest heads from yield plots in one replication to seed purification.
8	Multi-location testing. Grow 50-100 F$_{8:9}$ head-rows of lines still in test to produce pure seed.

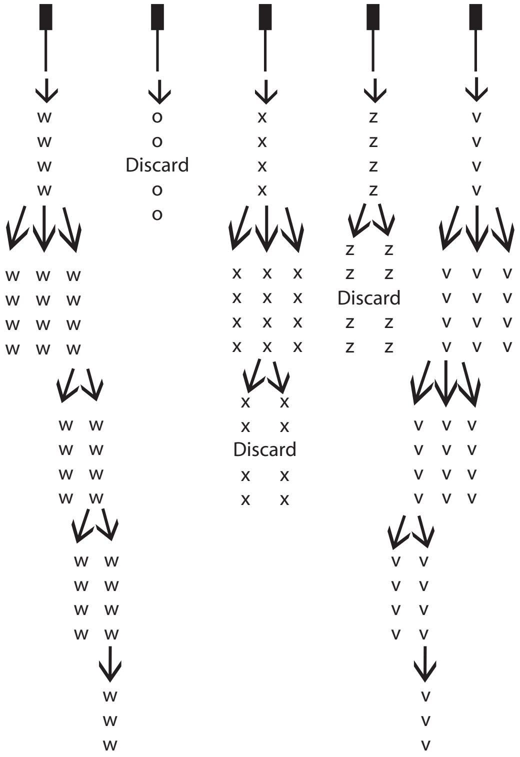
10.2.1 Origin

The term 'pedigree selection method' was applied when first used by Svalöf in Sweden

FIGURE 10.1

Diagrammatic representation of the pedigree method

Season	Procedure
1	Plant F_2 seed Select individual plants
2	Grow individual rows Select best rows Select best F_3 plants
3	Grow individual rows Select best families Select best rows Select best F_4 plants
4	Grow individual rows Select best families Select best rows Select best F_5 plants
5	Grow individual rows Select best families Harvest best rows in bulk
6	Extensive testing of F_5-derived lines



Courtesy of Fehr, 1987a

in 1891, where single plants were selected from an existing cultivar or a landrace population. Newman (1912) described how selected plants were laid out in the field as plant-row, ear-row or head-row plots. The Vilmorin Company in France developed the system independently, where it was termed the 'Vilmorin method of selection' (Fehr, 1987a).

10.2.2 Implementation

The method can be initiated or stopped at any generation during the inbreeding process. When combined with mass or bulk selection, it is generally applied in generations closer to when homozygote lines are developed. This is because other methods are less labour (therefore resource) intensive and easier to apply in earlier generations. Generally, selection starts with an F_2 population and goes on until homogeneous lines are developed. In the next cycle, the best $F_{2:3}$ lines are selected, followed by the selection of the desirable F_3 plants within each line. In all subsequent generations selection is performed on the most desirable families first, followed by the most desirable lines within that family, to finally select the best plants within each line, which are harvested individually (Figure 10.1).

TABLE 10.2

Expected additive genetic variability among and within lines during inbreeding process without any selection

Generation of lines	Additive Genetic Variability	
	Among Lines	Within Lines
$F_{2:3}$	1	1/2
$F_{3:4}$	1.5	1/4
$F_{4:5}$	1.75	1/8
$F_{5:6}$	1.875	1/16

Although breeding is a 'numbers game' – the greater the numbers managed, the higher the probability of finding the right or a better combination of genes – the size of the programme will always be limited by the resources available. This would include the level of the breeder's and support personnel expertise the institution is able to hire, land, hardware, technology and time. At the beginning of each season, the breeder should decide how many progeny rows they will be able to grow for all selection generations.

The pedigree method also relies heavily on the expected genetic variability in each generation, and that will determine the number of selections made (Table 10.2) (Fehr, 1987a). The genetic variability expected within each line is at a maximum at the $F_{2:3}$ generation, decreasing by half in each following generation.

10.2.3 Genetic background

The most important factor to be considered is the genetic variability present among and within lines during the inbreeding process (Table 10.1). Additive epistasis is generally much smaller than the additive portion of total genetic variability. Variability associated with dominance and dominant epistasis cannot be utilized in inbred lines. Dominance can complicate the selection of homogeneous and homozygous lines by not allowing differentiation of heterozygous individuals from dominant homozygous. The same can occur with the heterosis expressed by heterozygous individuals, slowing the homozygosity process (Fehr, 1987a).

10.3 PROS AND CONS OF THE PEDIGREE METHOD

10.3.1 Advantages of the pedigree method

- The 'art of breeding' can be extensively exercised. The breeder can effectively decide in the field the shape of the breeding programme and see the effect in every generation. Inferior genotypes can be discarded early in the process, allowing the use of higher volumes for early generations in the programme, and retaining only the good ones for the later, expensive, replicated experiments stage.
- Different locations and environments can be used in each growing cycle, allowing selection for different traits not expressed everywhere. Populations can be replicated in hot spots, i.e. environments where the desired selection traits are expressed at a maximum, to increase the probability of selecting for specific traits.
- The breeder can manage the amount of generic variance they want to keep within and between families, as well as the number of families.
- Different qualitative and quantitative traits can be selected at the same time in different generations, including traits being expressed at plant as well as grain level.

10.3.2 Disadvantages of the pedigree method

- Cannot be utilized in environments where genetic variability for the characters of interest is not expressed. If one cannot use off-season nurseries, there will be an associated increase in the length of time

for cultivar development compared with other methods of breeding.
- Considerable record keeping.
- An experienced person must do the selection (at least we flatter ourselves in thinking so).
- Requires more land and labour than other methods of inbreeding.

Besides the points above, there are questions concerning applied breeding programmes, especially those in the private sector. Questions about why the extensive data recording is needed, if the plants that are kept in the programme are there because they showed superiority anyway. Pedigree becomes difficult to use for quantitative traits, especially those with lower heritability. Despite the named disadvantages, that are more due to the different circumstances and priorities, this is the method that resulted in significant increases in the genetic gain in breeding programmes early in the twentieth century. The criteria would depend on how narrow the cross is, the heritability of the traits, costs of the evaluation, worth of the trait and resources available. Modifications were carried out once the system was understood, and it helped to acquire deeper knowledge of the high number of genes acting in plant development.

10.4 SINGLE-SEED DESCENT METHOD

Single-seed descent is a method to rapidly advance generations of inbreeding populations before starting the evaluation of individual lines, which is frequently used in conjunction with the pedigree method. The concept was proposed by Goulden in 1941. He noted that a breeding programme can be divided into two stages: the development of pure lines from segregating populations; and selection of desired pure lines from among those produced. The disadvantage of the pedigree method was that only one generation could be grown each year. By separating inbreeding from selection, the first process could be accelerated until homozygosity was reached. Working with wheat, he suggested that the number of progeny to be grown from a plant be one or two, growing two generations in the greenhouse in each autumn and winter, and one generation in the field during the summer. With this method, the F_6 generation can be reached in two years, compared with the five years needed with the Pedigree Method. Once homozygosity is achieved, a large number of lines can be tested for the desired traits.

The harvest of one seed from each plant during inbreeding was first described by Johnson and Bernard in 1962 for soybeans, and the first time this method was termed single-seed descent was by Brim (1966), who considered it to be a modified pedigree method.

The usual procedure is to harvest a single seed from each plant in a population, bulk the harvested seeds and plant the bulk in the next generation. The procedure can be started in the F_2 and continued until the desired level of homozygosity is achieved. The number of plants that will be needed in the last generation of inbreeding should be decided and the number of initial plants should be calculated backwards to the F_2 generation, taking into account the expected losses due to lack of germination.

In his book, Fehr (1987b) also describes modifications of the single-seed descent method, such as a multiple-seed procedure and a single-hill procedure. The objectives are the same: to obtain rapid generation advance. The methods are well suited for use in greenhouses and winter nurseries, where genotypes perform differently from their area of adaptation.

10.5.1 Advantages of the single-seed descent procedures

- They are easy to manage and speed up the inbreeding process as no special laboratories or techniques are needed in comparison with other methods, e.g. double haploid production.
- Procedures are well suited for environments where otherwise only one generation per year can be grown in the field.
- Can be less expensive than field selection where the costs of land and land management are high.

10.5.2 Disadvantages

- The size of the population should be adjusted for germination losses.
- All the F2 plants may not be present in the line evaluation due to germination losses, decreasing the genetic variance.
- The amount of seed available at the end of the inbreeding process is reduced, needing additional growing cycles just to multiply seed, thus delaying the total process.

REFERENCES

Brim, C.A. 1966. A modified pedigree method of selection in soybeans. *Crop Science*, 6: 220.

Fehr, W.R. 1987a. *Principles of Cultivar Development, Theory and Technique*. USA, Macmillan Publishing Co. 332 p.

Fehr, W.R. 1987b. Pedigree Method. *In* W.R. Fehr, ed. *Principles of Cultivar Development*. Vol. 1 Theory and Technique. USA, Mac Graw-Hill Inc.

Newman, L.H. 1912. Plant Breeding in Scandinavia. Canadian Seed Growers Association, Ottawa.

CHAPTER 11

Selection methods Part 3: Hybrid breeding

Donald N. Duvick*

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11.1 INTRODUCTION

When science-based plant breeding began at the beginning of the twentieth century, breeders at first produced only pure-line cultivars in self-pollinated species such as wheat (*Triticum aestivum* L.), or open-pollinated cultivars in cross-pollinated species such as sugar beet (*Beta vulgaris* L.). But following the success of hybrid maize (*Zea mays* L.) in the United States of America in the 1930s, breeders of field and horticultural crops began to look for ways to breed and produce hybrid seed of their own crops – crops other than maize. They usually intended to use hybrids to harness heterosis (see Chapter 2) and thereby produce higher yielding cultivars, but they also saw a potential for improving non-yield traits with more precision and breadth than could be achieved in either pure-line or open-pollinated cultivars. Additionally, seed companies saw commercial possibilities in hybrids. Growers would need to purchase hybrid seed every year because saved seed of a hybrid (F_2 seed) is significantly lower yielding than the hybrid parent, and it also may lack uniformity for important traits should such uniformity be necessary.

11.2 ORIGINS OF HYBRID BREEDING: CROP-SPECIFIC TECHNOLOGIES

11.2.1 Maize

Hybrid maize, made by crossing inbred lines of maize, was introduced to farmers in the United States of America in the late 1920s and early 1930s (Crabb, 1993; Jenkins, 1978). Maize breeders from both public and private sectors developed the first inbred lines and hybrid cultivars. Private seed companies produced and sold seed of the best hybrids. American farmers rapidly abandoned their open pollinated cultivars (OPCs) in favour of hybrids, even though they had to buy new seed every season (USDA-NASS, 2000). The best hybrids yielded more than the best OPCs, although not a great deal more, about +15 percent (e.g. Iowa State Department of Agriculture, 1934) . They also had stronger roots and greater resistance to stalk rot and subsequent stalk lodging. The farmers could easily distinguish the hybrids' advantages in standability.

North American farmers had begun to adopt mechanical maize harvesters ('corn pickers') on a large scale in the 1920s and 1930s; these farmers were attracted to maize hybrids because of the improvements in standability. Fewer lodged plants meant fewer ears missed by the corn picker, and therefore harvestable yield was increased significantly.

Two years of disastrous drought (1934 and 1936) in the United States Corn Belt gave further impetus to adoption of maize hybrids; the best hybrids were much more heat and drought tolerant than the OPCs. The author's personal experience is that, in 1936, on our home farm in Illinois, the advantage of hybrid over local OPC was so great that the high school vocational agriculture instructor brought his class out to see this on-farm demonstration of the superior drought tolerance of hybrid maize (then a new and rather mysterious crop). Our OPC was essentially 100 percent barren and was used only for fodder; the hybrid made enough grain to warrant harvesting. There was a concomitant effect in the seed trade.

A common statement in those days was that every dollar spent on hybrid seed should produce extra grain yield worth at least three dollars. Fortuitously in the 1930s, the federal government instituted measures to support the price of maize grain. This gave farmers confidence that they could get a fair return for their extra grain yield. Before support prices were

> *Hybrid 307 was the double cross that I would say really put us in the seed-corn business. A lot of farmers knew about hybrid corn by that time and some of them were piddling around and trying a little bit of this and a little bit of that. Most of them waited to see what happened; they didn't think it would really amount to anything. We put out some of the hybrid in 1936 and it was so drought resistant that it convinced a lot of people that hybrid corn was something they wanted to grow.*
>
> (R. Baker, pers. comm., 1990)

instituted, maize grain prices (in the midst of the Great Depression of the 1930s) were so low that farmers might have decided against spending money on hybrid seed despite its extra yield, reasoning that the return on investment in hybrid seed might not be realized.

Seed production of hybrid maize was relatively simple because of the separation of male and female flowers: male in the tassel and female in the ear. Rows of detasselled plants could be used as seed parents ("female") to be pollinated by adjacent rows of non-detasselled plants ("male") of a different genotype. No other crop had such phenotypic advantages; breeders of other species therefore knew they had to look for other ways to produce hybrid seed efficiently and economically.

11.2.2 Horticultural crops

Genetic investigations in horticultural crops suggested several methods with the potential to make hybrid seed economically, at prices farmers could afford (reviewed in Duvick, 1966).

Cytoplasmic-nuclear male sterility was discovered in crops such as onion (*Allium cepa* L.) and beets (*Beta vulgaris* L.), and breeders of those crops soon developed hybrid cultivars. Sterility resulted from interactions between a specific cytoplasmic genotype and a specific nuclear genotype. Plants with sterile cytoplasm plus nuclear non-restorer genes were male sterile; plants with sterile cytoplasm plus nuclear restorer genes produced fertile pollen (fertility restoration). In contrast to plants with sterile cytoplasm, plants with normal cytoplasm were male fertile when they carried either of the nuclear genes: restorer or non-restorer. Fertility restoration was not needed for onion and beet hybrids, grown for their vegetative parts, but it was needed when cytoplasmic male sterility was used to make hybrids of crops grown for fruit production.

Hybrid seed production required efficient methods of cross-pollination to keep costs of production (and thereby seed prices for the farmer) at economically low levels. Bees did the pollination for onions, and wind served for beets.

Self-incompatibility, present in several species of horticultural crops such as broccoli and cabbage (*Brassica oleracea* L.) was used to make seed of hybrid cultivars. The term 'self-incompatibility' as used here means the inability of a plant to set seed when self pollinated, even though it can form normal zygotes when cross-pollinated, and its pollen can fertilize other plants. Breeders used two types of self-incompatibility: gametic and sporophytic, depending on which kind prevailed in a given crop species. Nuclear genes govern both types, and genetic interactions can be complicated but manageable for development of lines to be used as seed parents or pollinators.

Hand emasculation followed by hand pollination was (and still is) used to make hybrid seed of some horticultural crops, for example eggplant (*Solanum melongena* L.) and pepper (*Capsicum annuum* L.). Despite high inputs of labour, it was used successfully to make hybrid seed of crops with high value, relatively low seed requirements, and relatively abundant seed numbers per pollinated flower. Hybridization via hand emasculation was often performed in developing countries with relatively low labour costs, to lower the cost of seed production.

Genetic male sterility was used to make hybrid seed of a few crops (e.g. pepper), although, like hand emasculation, its use required considerable inputs of hand labour. Segregating populations of heterozygous lines could be grown as female; pollen-fertile plants would be removed at the time of flowering, or earlier if they could be identified with a linked marker gene.

Monoecious (male and female organs on the same plant but in different flowers), *gynoecious* (plants with only female flowers) *or andromonoecious* (plants with both bisexual and male flowers) *genotypes*, common in some families such as the melons (Cucurbitaceae), were manipulated to produce hybrid seed, using bees as pollinators, or sometimes with hand pollination (made easier because hand emasculation is not required). An example in cucumber: a gynoecious inbred used as female might be crossed to a monoecious inbred used as male, with bees as pollinators (Janick, 1998). Chemicals can be used as hybridizing aids in some species. “Ethylene-producing compounds (Ethrel), sprayed on squash plants, turn a monoecious plant into a gynoecious plant by turning all flowers into female.” (R. Heisey, pers. comm., 2005)

In summary: a variety of methods have been developed and are now employed to produce seed of hybrid cultivars of vegetable crops. Choice of a specific method depends on the species and how it is utilized. Growers of horticultural crops in industrialized nations have adopted hybrids extensively. For example, in North America in 1996, 21 of 24 vegetable crops were grown as hybrids, to varying extents (Janick, 1998). The proportion of crop area planted to hybrids varied by crop; at the two extremes, celery (*Apium graveolens* L.), lettuce (*Lactuca sativa* L.) and radish (*Raphanus sativus* L.) were 0 percent hybrid, whereas broccoli and Brussels sprouts (*Brassica oleracea* L.), pickling cucumber (*Cucumis sativus* L.), muskmelon (*Cucumis melo* L.) in the Eastern United States of America, and spinach (*Spinacea oleracea* L.) were 100 percent hybrid. Hybrid use in horticultural crops has expanded more slowly in the developing countries than in the industrialized countries but in recent years the area planted to hybrid vegetable cultivars of several species has expanded markedly in a number of developing countries, for example in countries of Southeast Asia (Kunz, 2002). In developed countries, probably more than 90 percent of the tomato and pepper seed sold is hybrid. In developing countries, the shift is to hybrid varieties. (R. Heisey, pers. comm., 2005). Yield gains can be dramatic when good quality seed of hybrids adapted to a developing country become available (M. Jahn, pers. comm., 2005).

11.2.3 Field crops

Farm production of field crops such as sugar beet, rye (*Secale cereale* L.), wheat, barley (*Hordeum vulgare* L.) sunflower (*Helianthus annuus* L.), and grain sorghum (*Sorghum bicolor* (L.) Moench.) requires large amounts of seed for planting the crop and return per unit area is relatively low compared to most horticultural crops, so expensive labour-intensive methods of producing hybrid seed (such as hand emasculation) were ruled out. Breeders of field crops sought to develop hybridization techniques in which seed parents and pollinators could be grown on a field scale, and therefore looked to cytoplasmic male sterility and, to a lesser extent, to self-incompatibility or other genetic systems that could be used on a large scale. Pollination also needed to be on a field scale, such as with wind or with bees. Successful hybridization via wind pollination required that males shed abundant amounts of pollen and female lines be receptive (e.g. florets should open at appropriate times). Finally, fertility restoration in the final hybrid as grown by farmers was essential for grain crops such as sorghum, sunflower, wheat or barley.

Cytoplasmic-nuclear male sterility was used successfully to produce hybrid cultivars of several field crops, starting with crops such as grain sorghum and sugar beet, and followed by (among others) rye, pearl millet (*Pennisetum glaucum* (L.) R. Br.), sunflower, canola (*Brassica napus* L. and *Brassica rapa* L.), and rice (*Oryza sativa* L.) (Axtell *et al.*, 1999; Brown, 1999; Canola Advantage, 2005; Duvick, 1966; Geiger and Miedaner, 1999; Miller, 1987; Owen, 1945; Renard *et al.*, 1998; Stephens and Holland, 1954; Virmani, 1994; Yuan, Yang and Yang, 1994). Cytoplasmic male sterility was also used on a large scale to make maize hybrids in the United States of America in the 1950s and 1960s, but its use was greatly curtailed following the 1970 epidemic of race T of Southern corn leaf blight (*Bipolaris maydis* (Nisikado & Miyake)) (NRC, 1972; Tatum, 1971).

Hybrid wheat has been bred and produced via cytoplasmic male sterility or with chemical hybridizing agents, application of which causes pollen sterility in a line intended as seed parent in a seed production field. The resulting hybrids are male fertile. It has shown limited success, in part because of low and highly unpredictable seed yields in hybrid seed production fields and in part because heterosis within a given class of wheat contributed unacceptably small yield gains in relation to cost and reliability of seed production (Jordaan *et al.*, 1999; Knudson and Ruttan, 1988; Koemel *et al.*, 2004). Nevertheless, hybrid wheat, produced via cytoplasmic male sterility or chemical hybridizing agents, has been successful in some regions of the world (Nicolas, 2005; Saaten-Union, 2005).

> *We … have a quite successful hybrid wheat programme today in South Africa based on [cytoplasmic male sterility]. The hybrids do better than varietals in stress environments and yields are acceptable …*
>
> (T. Crosbie, pers. comm., 2005)

As with horticultural crops, industrialized countries led the way in adoption of hybrid field crops and a number of the developing countries followed closely behind them. Crops such as grain sorghum, maize[1], pearl millet, sunflower and rice are now widely grown as hybrids in many of the developing countries (e.g. Axtell *et al.*, 1999; Ejeta, 1988; Guohui and Longping, 2003; Joshi *et al.*, 2005; Swastika *et al.*, 2004; Virmani, Mao and Hardy, 2003).

Rice hybrids made with cytoplasmic-nuclear male sterility have been grown for several years in both developed and developing nations. China led the way; IRRI was influential in extending the technology to tropical Asia (Virmani and

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[1] In Asian countries, excluding … China approximately 40 percent of [maize] is planted with hybrids. In Asian countries including … China approximately 76 percent of [maize] is planted with hybrids. (T. Kunta, pers. comm., 2005)

> *Many countries plant a high percentage of [sorghum] hybrids. In the USA, Mexico, South America, Australia and South Africa the percentage of hybrids is close to 100 percent. In India's rainy season it is close to 80–90 percent hybrid. In the post-rainy [season] they plant an OPV … almost 100 percent of which is used for local consumption … Only in many sorghum growing areas of Africa have hybrids not taken off … .*
>
> (K. Porter, pers. comm., 2005).

> *In Asian countries, excluding … China, approximately 40 percent of [maize] is planted with hybrids. In Asian countries including … China approximately 76 percent of [maize] is planted with hybrids.*
>
> (T. Kunta, pers. comm., 2005)

> *Hybrid cotton makes up about 15 percent of the Chinese acreage and 45 percent of the acreage in India. … The hybrid cotton in China appears to be increasing. A small amount of F_1 intraspecific and interspecific hybrids are grown in the USA. … The hybrids are produced by hand, probably in India and marketed by an Israeli company.*
>
> (W. Meredith, pers. comm., 2005)

Kumar, 2004). In recent years a special kind of genetic male sterility has been used as well, to make 'two-line' hybrid rice (Guohui and Longping, 2003; Yuan, 1998). Seed is produced on female inbred lines that are homozygous for environmentally sensitive recessive male sterility genes. Seed production fields are planted in an environment (e.g. long day and/or high temperature) that enables expression of the male sterility gene and thus enables successful seed production. Seed increase fields of the female lines are grown in an environment (e.g. short day and/or cooler temperatures) that represses expression of the male sterility genes, allowing the female lines to reproduce via self-pollination.

Cotton hybrids are widely grown in India, and also in China and Viet Nam), but very little elsewhere (Anonymous, 2005; James, 2002; Meredith, 1999; Roberts, 2005).

The Indian hybrids are produced by means of hand emasculation and pollination. The cost of labour for hand emasculation and pollination is prohibitively high in developed nations. Although genetic systems such as cytoplasmic-nuclear male sterility are present in cotton (Meredith, 1999), to date none of them have been used to make hybrid cotton on a large scale.

Soybeans (*Glycine max* (L.) Merr.) are not grown as hybrids, although nuclear and cytoplasmic-nuclear sterility systems have been reported as operational in the crop (Ding *et al*., 2002; Smith, Horner and Palmer, 2001). Effective cross-pollination systems must be developed (probably using insects such as honeybees (*Apis mellifera* L.) or leaf cutter bees (*Megachile rotundata* F.) and modified soybean flower morphology), to enable adequate levels of seed yield (Palmer *et al.*, 2001).

In theory one could produce apomictic hybrids of important field crops such as rice or maize; seed multiplication would be much less expensive and hybrids could be sold at lower prices. Additionally, farmers could reproduce the apomictic hybrids via saved seed as they now can do with pure-line self-pollinated crops. Research is underway to develop apomictic hybrids but the genetics are complicated.

Development of apomictic hybrids will require extensive research and experimen-

> *The components of apomixis comprise the absence of meiosis (apomeiosis), embryogenesis in absence of fertilization (parthenogenesis) and functional endosperm development … Reports on the genetic control of apomixis are often contradictory and show no clear consensus on the number of genes involved in the phenomenon. … The fact that most apomicts studied to date have suppressed recombination suggests that apomixis or apomeiosis is controlled by a tightly linked gene complex.*
>
> (Perotti *et al.*, 2004)

tation (Bi *et al.*, 2003; Hanna, 1995; Perotti *et al.*, 2004).

In summary, several of the major field crops in developed countries are grown extensively and often exclusively as hybrids. For example, maize, sunflower and grain sorghum are essentially 100 percent hybrid, and the area planted to hybrid rice and hybrid canola is growing rapidly. These same crops increasingly are grown as hybrids in a number of developing countries.

11.3 ADVANTAGES OF HYBRIDS

11.3.1 Increased yield and profitability for grower

For most crops, the best hybrids outyield the best non-hybrid cultivars, when both types are adapted to local conditions (Coors and Pandey, 1999; Pixley and Bänziger, 2004). Hybrids of self-pollinated crops benefit from an added component of yield: heterosis (hybrid vigour), unless the parents are very similar genetically. Hybrids of open-pollinated crops possess in reproducible form the higher yielding genotypes from among the wide range of hybrid genotypes present in any open-pollinated cultivar or improved population, and therefore the best hybrid will outperform the best OPC.

As noted above, farmers plant hybrids when the added income from higher yield of the hybrid more than compensates for the cost of the new seed required for each planting. The added income may be in-kind (as when the product is used directly as food or as animal feed) or in cash (when the product is sold on the market).

A caveat: the hybrids must be well adapted to the farmer's location and they must have preferred requirements in quality or other traits.

A second caveat: farmers will require that seed supplies (and suppliers) be reliable; seed deliveries must be adequate and timely, and seed must be of stated quality. In addition, commercial markets for the farmer's crop must be reliable and with adequate prices. If any of these criteria are not met, farmers will not use hybrid seed.

11.3.2 Increased dependability of performance

Successful hybrids are more tolerant of abiotic stress than the OPCs that they replace (e.g. Axtell *et al.*, 1999; Haussmann *et al.*, 2000; Menkir and Akintude, 2001; Pixley and Bänziger, 2004). They out yield the OPCs in stressful as well as high-yield environments in the location for which they are bred. In part this advantage is because heterosis *per se* can increase stress tolerance (e.g. Duvick, 2005; Mojayad and Planchon, 1994). But increased stress tolerance is also the inevitable product of breeding and selection for dependability of performance in the location where the hybrids are to be grown (Ejeta, 1988; Tollenaar and Wu, 1999). The most dependable hybrids, by definition, outyield other cultivars in low-yield as well as high-yield years, in unfavourable as well as in favourable growing sites

(Duvick, 1997). One should note that augmented stress tolerance as a result of breeding for dependability is not unique to hybrid breeding programmes. Breeding for dependable performance improves abiotic stress tolerance of non-hybrid as well as of hybrid cultivars (Rajaram, Singh and Ginkel, 1997; Smale *et al*., 2002), although heterosis *per se* plus ability to combine tolerance traits from two parents into one hybrid does give a unique advantage to hybrids.

A caveat: Breeding for tolerance of abiotic stress at one location does not necessarily give adequate tolerance to that stress in a markedly different location (e.g. the different locations may have a much greater intensity of the targeted abiotic stress, such as drought at flowering time).

11.3.3 Uniform expression of desired traits

Uniform expression of certain traits is highly desirable for some crops. Such uniformity is automatic in the case of cultivars of self-pollinated crops such as tomato or wheat, but not so for cross-pollinated crops such as maize or beets. Hybrids of cross-pollinated crops are uniform for all traits if the hybrids are single-cross hybrids, made by crossing two inbred lines. Thus, hybrids in cross-pollinated crops present new opportunities for producing a uniform product, if uniformity is desired or required, as in many horticultural crops (Wehner, 1999).

11.3.4 Greater range of useful traits

Where important traits (such as disease resistance) are controlled by dominant genes, a hybrid can contain (and express) the dominant genes from both of its parents, when neither of them has the full set of needed dominant genes (Wehner, 1999). The hybrid therefore will have better protection than either of the parents (more tolerance to biotic stress), and the goal of broad protection is reached in one generation rather than the long-term back-crossing and selection needed to place all of the needed genes in a single, inbred cultivar.

11.3.5 Customers can dictate traits of hybrid cultivars

Farmers who plant hybrid seed can dictate the traits of the hybrids they plant, if they buy the seed from commercial firms. Because the existence of commercial seed companies depends on seed sales, they must develop hybrids (or produce seed of hybrids developed by the public sector) that the customer wants to buy. For example, the hybrids must be adapted to the environment and farming practices of each adaptation region where the seed is to be sold, and additionally the hybrids must have specific traits and quality as desired by farmers, their potential customers.

Farmers may favour (or insist upon) maize hybrids with resistance to prevalent leaf diseases in their region, sorghum hybrids with tolerance to iron deficiency in alkaline soils common to their region, or rice hybrids with flavour and texture that suits their taste (or the taste of the ultimate consumers of their product). In the United States of America, during the past 70 years, maize breeders continually have had to breed hybrids with ever increasing tolerance to the stresses imposed by higher plant densities,

> *Scale of farmers is not that important. It is the desirable traits which farmers consider as important. If they are satisfied with the traits of the product, they do not mind buying [hybrid rice] seeds every year.*
>
> (H. Miah, pers. comm., 2005)

as farmers have gradually increased the plant density of their maize fields, from ca. 30 000 plants per hectare in the 1930s to the current 80 000 plants per hectare or greater (Duvick, 2005). Companies that fail to develop or distribute locally adapted hybrids with desired traits may fail as business entities, especially if competitor companies succeed where they have failed. Thus, the customer is in charge; breeders must do their best to furnish what the farmer wants and needs. [This is a clear example that client-oriented breeding does not necessarily include farmer participation. Editors.]

A caveat: if seed companies choose to not breed hybrids for a particular crop or region, farmers cannot force them to do so; in this case, public-sector breeding is essential if the farmers are to have hybrids [or farmers may be trained to produce hybrids for themselves. Editors].

11.4 DISADVANTAGES OF HYBRIDS

11.4.1 Annual capital investment by grower (seed purchaser)

Seed of hybrid cultivars must be purchased for each planting. As noted above, cash or credit must be available to farmers who wish to plant hybrids, and if that is lacking the farmer cannot grow hybrids. A corollary to shortage of cash is lack of a dependable and adequately priced market for the product. If the market is unstable, or offers prices that are too low, farmers will not make annual investments in hybrid seed. Such non-investment applies equally to other inputs requiring outlays of scarce cash or credit.

A second consideration is related to the kind of environment in which the crop is to be grown. Farmers may choose to not spend money on hybrid seed for planting in a potentially very unfavourable season (e.g. in the dry season in a region with alternating well-watered and very low rainfall seasons).

> *During winter season when … maize productivity is high, farmers in Bihar and eastern Uttar Pradesh in India, and in Bangladesh, are ready to buy hybrid seed, even though it is expensive. The same farmer will not plant hybrids in the same field during the summer season when risks of drought and floods are high and the chances of losing the crop are higher.*
>
> (G. Srinivasan, pers. comm., 2005)

Even though they plant hybrids in the favourable season, they will not do so in the unfavourable season; e.g. maize plantings in wet versus dry seasons in Lampung, Indonesia (Swastika *et al.*, 2004). They plant saved OPC seed in the risky (drought and/or floods) season because they know from experience that the crop may be totally lost or at best the yields may be so low that the cost of hybrid seed will not be matched by the value of extra yield of the hybrids. Similar considerations hold for farmers who grow their crop in other kinds of low-yield, risky environments (Pixley and Bänziger, 2004).

One might wonder why these farmers would not plant drought-tolerant hybrids instead of OPCs (presumably less tolerant to drought) in the unfavourable, dry season. Quite simply, the astute farmers know that their 'dry' seasons can be so disastrously dry that no amount of drought tolerance would suffice. They know that tolerance is not synonymous with immunity. The investment in hybrid seed would thus be totally lost. And even if the crop made some grain, the extra yield from the hybrids probably would not be enough to pay for the cost of the hybrid seed, as mentioned above.

11.4.2 Potential uniform susceptibility to new pest genotypes

As stated earlier, most hybrid genotypes are highly uniform. This means that they may be uniformly resistant to important diseases or insect pests, but they also may be uniformly susceptible to new and unexpected pests, or to an unexpected and highly unfavourable growing season.

This condition is not unique to hybrid cultivars; it is present and presents the same potential problems in self-pollinated crops such as wheat or soybeans (Simmonds, 1993; van der Plank, 1963). And even genetically heterogeneous crops—or wild plant species—can be devastated by a new genotype of insect or disease if they happen to lack the needed resistance or tolerance genes, despite their highly heterogeneous nature. Thus, Dutch elm disease (*Ophiostoma ulmi* Buisman) devastated the genetically diverse populations of native American elm (*Ulmus americana* L.) in the United States of America in the1960s (French *et al*., 1980). Chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) overwhelmed the entire wild population of American chestnut trees (*Castanea dentate* (Marsh.)) in the mid-twentieth century (Anagnostakis, 2005). Ergot (*Claviceps purpurea* (Fr.) Tul.) infestations of rye (a genetically heterogeneous cross-pollinated crop) caused numerous epidemics of poisoning in Europe during the Middle Ages and in more recent centuries as well (Matossian, 1989). And many centuries before those events, the early Romans annually sacrificed a red dog to the god Robigus in hopes that he, sufficiently satisfied with the red dog, would not ravage their fields of genetically heterogeneous wheat cultivars with epidemics of red rust (*Puccinia* spp.) (see Large, 1982 for this and other narratives of destructive plant disease epidemics that resulted in widespread famine and great hardships for millions in the past). Genetic diversity can help, but it is not a cure-all.

Within any one season, farmers who plant uniform hybrids can spread their risk by growing several hybrids of differing parentage, more or less as when one grows a genetically heterogeneous non-hybrid cultivar. In addition, breeders constantly develop new hybrids of genotypes different from the predecessor hybrids, and thereby provide farmers with ‘genetic diversity in time’, also called temporal genetic diversity (Duvick, 1984; Smale *et al*., 2002). Also, as noted above, hybrids in self-pollinated crops can contain a broader range of resistance genes (greater internal genetic diversity) than is easily bred into individual pure-line cultivars.

Ultimately, however, one must recognize that to grow hybrids of cross-pollinated crops is to reduce the genetic diversity in the field, in comparison with growing highly heterogeneous OPCs of those same crops.

11.4.3 Difficult to serve unique small adaptation areas

Seed companies usually cannot afford to breed and produce seed for very small, specialized markets. Farmers may therefore be unable to find commercial hybrids that suit their needs if they are in a small region with

> *The challenge in developing countries is that [some farmers] have no or very limited choice because seed of improved [sorghum] varieties or hybrids is not available. Clearly, there are local preferences but it may be impossible for large companies to adequately address all of them.*
>
> (K. Porter, pers. comm., 2005)

unusual growing conditions or special quality requirements (unusual soil type, special cooking quality, etc.) (Paudyal *et al*., 2001).

One should note that professional breeding of crops of any kind—public sector or private sector, hybrid or non-hybrid—is likely to by-pass farmers in small, exceptional adaptation areas. The problem is not unique to hybrids; rather, the problem is that funds for breeding are always in short supply compared to the needs globally. Breeders, both public sector and private sector, ordinarily choose to breed for regions that hold the largest potential to use their products. As (or if) public funding or seed company sales prospects increase, the professional breeders gradually can afford to serve smaller and smaller adaptation areas. An advantage of public breeding organizations is that they intentionally can allocate scarce resources to breeding hybrids for farmers not likely to be served by the private-sector breeders (Bänziger *et al.*, 2004; Hassan, Mekuria and Mwangi, 2001).

11.5 BREEDING METHODOLOGY

11.5.1 Assembling and enriching breeding populations

Breeders of hybrid crops assemble and enrich breeding populations in ways that are not substantially different from those used by breeders of non-hybrid crops. When professional breeding gets underway in a new area, breeders usually use the best locally-adapted landraces for initial breeding and selection. Breeders of hybrids may develop a first generation of inbred lines from the selected landraces and, as well, form new populations (often enriched with elite germplasm from other locations) to be subjected to continual selection and improvement. They then use the improved populations or crosses among the first-generation inbreds for further breeding and selection, and the cycle continues. Breeders at CIMMYT have used such methods to select drought tolerant maize for the tropics and sub-tropics; these improved populations then have been the source of inbred lines that can be the parents of superior hybrids (Bänziger, Edmeades and Lafitte, 1999).

> *At CIMMYT we have [maize] gene pools and advanced populations which are derived from gene pools. Gene pools are broad based, formed from germplasm accessions, local varieties and diverse sources. We work with mild selection in gene pools [and] stringent selection pressure in population improvement (recurrent selection). We derive lines from [improved populations] and advance them as inbreds for further testing. At the same time, we also [practise] pedigree breeding in a limited scale.*
>
> (G. Srinivasan, pers. comm., 2005)

It is not unusual for breeders of horticultural crops to make very wide crosses, such as interspecific crosses, to bring in novel traits (Rick and Chetelat, 1995; Tanksley *et al.*, 1996). This occurs with field crops as well: sunflower, maize and barley, for example, are crossed with wild relatives to bring in useful genes (Arias and Rieseberg, 1995; Grando, von Bothmer and Ceccarelli, 2001; Pons, 2003; Seiler, 1992; Whitt *et al*., 2002). Again, this practice is not unique to hybrid breeding but as noted above, introgressed genes may be used more easily in hybrids.

11.5.2 Inbred line development

Breeders produce uniform inbred lines to use as parents of hybrid cultivars by performing self-pollination in improved populations or in crosses of elite inbred lines (usually, lines that were parents of

> *Most of [maize] breeding populations are from pedigree breeding, some from backcrossing, little with improved populations.*
>
> (T. Kunta, pers. comm., 2005)

> *To a large extent we use pedigree breeding [for tomato and pepper], using elite hybrids. … We will occasionally use backcrossing if we want to introgress a new trait or disease resistance.*
>
> (R. Heisey, pers. comm., 2005)

> *In canola, most breeding programmes use doubled haploidy as a method of inbred development. However, pedigree breeding is still used in canola. Two-way, three-way and complex crosses are produced to generate inbred lines. Utilization of genetically broad populations or synthetics to extract inbred lines is not that common in canola. Backcrossing is mostly used in trait transfer.*
>
> (J. Patel, pers. comm., 2005)

successful hybrids). The latter method is called pedigree breeding, and for most crops it is the most widely used method for inbred development because it has higher odds of producing improved new inbred lines. At the same time, superior inbreds from improved populations (even if few in number) can bring in radically new and useful genotypes and form the basis for new advances in pedigree breeding or population improvement; thus, both methods are needed for continuing forward progress in a breeding programme.

Inbreds are selected for desired phenotypic traits during selfing generations. In field crop breeding they also are evaluated in test crosses (crosses to proven inbred lines) in order to select those with the best combining ability for yield and other important traits. The best lines from those small-plot trials are then crossed to other superior inbred lines to produce experimental hybrids that will themselves undergo several rounds of testing and elimination. Finally, a favoured few of the experimental hybrids will be chosen for introduction as new commercial hybrids.

At present, commercial hybrids of most crops are single-cross hybrids, i.e. a cross of two inbred lines. However, the first maize hybrids in the United States of America (1930s) usually were double-cross hybrids (cross of two single-crosses) or occasionally three-way crosses (single-cross female × inbred male). The double-cross method was used because the earliest inbred lines had very low and unpredictable yields and as a consequence the expense of producing single-cross seed was prohibitively high. Using a single-cross as a seed parent allowed production of hybrid seed at prices farmers could afford (Jones, 1918; Jones, 1922). Subsequent generations of inbred lines had incremental increases in yield (e.g. Duvick *et al*., 2004); eventually, inbred yields were high enough to allow the use of inbreds as seed parents for production of single-cross hybrids, hybrids that could be produced and sold at prices farmers could afford. Interestingly, a similar pattern has been followed with hybrid carrot (*Daucus carota* L.); later-generation inbred lines are more vigorous than the earliest generations, and

> *Since canola is an oilseed crop with quite a few important quality traits … in breeding nurseries we select for … high oil, high protein, low glucosinolates and low total saturated fatty acids.*
>
> (J. Patel, pers. comm., 2005)

thereby enable production of single-cross instead of three-way hybrids (Simon, 2000).

An exception to the progression toward single-cross hybrids can exist in regions with extremely low yield potential for field crops such as maize. In such situations, the lower yield potential of a double-cross hybrid (compared to the best single-crosses) may be acceptable if the lower seed price of the double-cross more than compensates for its lower yield (Hassan, Mekuria and Mwangi, 2001).

11.5.3 Assignment of inbreds to parental groups

As hybrid breeding programmes mature, breeders tend to sort inbreds into two or more groups based on their complementary interactions (Melchinger and Gumber, 1998).

Maize breeders called these groups ‘heterotic groups’, with the assumption that maximum heterosis for yield is achieved when inbreds from complementary groups are hybridized. At the least, inbreds in one group have a minimal genetic relationship with those in other groups, and so inbreeding depression is avoided when lines from one group are crossed with those of another. Perhaps a more provable reason for formation of the contrasting groups is that inbreds from one group can supply strength in traits that are not expressed or weakly expressed in inbreds of the other group (Tracy and Chandler, 2004). Thus one group might contribute better seed quality traits (and make good females), the other group might be better at pollen shed (and make good males). Or one group might contribute dominant resistance to certain disease or insect problems and the other group might contribute dominant resistance to a different set of important disease or insect problems. The hybrids would express the dominant traits of both sides and therefore would have a range of resistance greater than any of the inbred lines.

> *We take [sorghum] lines through a year of topcross, then move [them] to more wide area testing in more hybrid combinations. That will continue for 2–3 years and then we move to larger-scale testing in farmers’ fields (strip trials) before release. Most companies do the same. Hybrids are screened in various screening trials for disease and insect resistance, lodging, drought screens, etc. Yield measurement is done at all stages of testing.*
>
> (K. Porter, pers. comm., 2005)

> *[We] use heterotic [single cross] testers ($A_1 \times A_2$ and $B_1 \times B_2$) which in the wider sense match the Tuxpeño/ETO pattern and have been chosen due to their excellent general combining ability, in addition to their excellent specific combining ability with each other.*
>
> (M. Bänziger, pers. comm., 2005)

Similar situations can exist in other crops, both field and horticultural. In some horticultural crops such an increased range of useful traits is the chief reason for making the hybrids; a hybrid may show very little heterosis for yield *per se* but it will have a greater range of desirable traits than is found in either of its non-hybrid parents.

11.5.4 Hybrid formation, trials and evaluation

Experimental hybrids are tested in various ways before some of them are chosen for production and sale to farmers. Breeders of field crops typically will test large numbers

> *Since there is minimal heterosis … in tomatoes and peppers … we do not try to make up heterotic groups. … We do however look for combinations of parental lines that exhibit "specific combining ability" for what I refer to as "economic heterosis". … An example of [economic heterosis] in tomatoes is the trait of "heat set" for the Florida growers, where a parent line with small fruit but which sets well under high temperatures is crossed with a line with very large fruit which sets poorly under high temperatures. The hybrid would have fruit of acceptable size, and moderate levels of set under high temperatures.*
>
> (R. Heisey, pers. comm., 2005)

> *Very extensive yield trialling [of maize hybrids] across the [Asia-Pacific] region; … minimum of 4–5 years and across representative areas/environments (30–50 locations per year at pre-commercial stage) … before releasing."*
>
> (T. Kunta, pers. comm., 2005)

of experimental hybrids in two or more seasons of small-plot yield trials, discarding all those that do not meet predetermined levels of excellence for yield and other necessary traits such as tolerance to locally important abiotic and biotic stresses. Trials are grown not only at the breeder's research station but also on farm fields distributed about the locations where the hybrids will be grown commercially. This ensures that trials are grown with management typical of that used by local farmers, as well as giving opportunity for the breeder to monitor performance of the experimental hybrids in the local environment.

Some of the trials may be conducted in "managed stress environments" to enable greater intensity of selection for tolerance to critical stresses (e.g. drought) of the target region (Bänziger *et al.*, 2004; Edmeades, Bänziger and Cortes, 1997).

During the performance trials, hybrids are rated for quality traits that are important for the crop, such as flavour and texture in rice, or oil quality in canola. After two or three seasons of small-plot yield trials, the surviving hybrids, now becoming potential commercial hybrids, are field-produced in limited quantity and distributed to farmers for evaluation by farmers (and breeders) at field scale under farmer-managed conditions. Finally, those few hybrids that have shown superior performance for all needed traits in both small-plot and farmer trials will be released and offered for sale. An essential element of "superior" performance is "reliable" performance; the hybrids must outperform other cultivars in both good and bad growing conditions of the adaptation area in which they are to be sold.

Such detailed testing may not be performed when hybrids are first offered for sale in a new region or country. Hybrids that are adapted to similar environments elsewhere will be introduced in limited amounts and those that do best will be sold in larger quantity (should there be demand for them). As (or if) the market grows, local breeding and testing programmes may be instituted to increase the numbers and adaptation of hybrids for the region.

Breeders of horticultural crops follow trial regimes similar to those for field crops except that they may move promptly from initial trials on their own research facility to distribution of limited amounts of experimental hybrids to producers, sufficient for the farmers to grow and evaluate the hybrids on a field scale. The farmers can compare the experimental hybrids with their current favourite cultivars and report their findings to the breeder (R. Heisey, pers. comm., 2005).

11.6 SEED PRODUCTION

11.6.1 Technical aspects

Seed production techniques, such as detasselling, cytoplasmic male sterility, hand emasculation and pollination, and various kinds of self-incompatibility, have been discussed earlier.

All of the methods that use pollination by wind or insects on a field scale share a common need: to establish sufficient isolation from other sources of pollen to ensure that out-crossing is held to acceptably low levels. For some crops this can mean that seed production fields must be long distances from other fields of that crop.

Seed producers also must ensure that seed has satisfactory germination, is produced in sufficient quantity to satisfy farmer needs, and, importantly, is delivered in timely fashion, suited to the planting schedules of the farmers who use the seed. Truthful labelling is essential as well; this may seem to be an unnecessary statement, but in some parts of the world seed has been sold as first-generation hybrid when it was not. This seriously damages farmers' impressions of the value of hybrid seed and the veracity of seed companies (e.g. Ilagan, 2004) [and is particularly frequent in developing countries where Governmental Seed Companies have the monopoly of seed production and distribution. Editors].

Efficient and accurate performance of these multiple tasks requires skilled workers, specialized equipment, and, above all, a well-coordinated and well-directed organization, i.e. a hybrid-seed production company.

> *Testing [in sunflower] is necessary in all the zones of the world, mainly because each zone has some particular abiotic or biotic stress that needs to be assessed. Thus it is done in North America, throughout the sunflower growing regions of Europe, South America, India, Australia and other parts of Asia. Selection time from inbred genesis to culminating hybrid products can take a total of up to 10 years.*
>
> (G. Cole, pers. comm., 2005)

11.6.2 Seed producers

One should note that although public-sector breeders (e.g. academic institutions, government agencies or international research centres) do hybrid breeding (i.e. they may produce improved populations, inbred lines and well-tested final hybrids), the large-scale production and distribution of hybrid seed to farmers is nearly always the work of commercial seed companies.

Public-sector breeders (via the institutions that employ them) will release their plant breeding products for use by the private sector, using a variety of forms of release. In some cases, no restrictions are placed upon the released germplasm; in other cases, some sort of intellectual property protection is used to allow collection of royalties or other forms of payment (e.g. Butler and Marion, 1985; ERS, 2004; Heisey, Rubenstein and King, 2005; University System of Maryland, 2004).

Seed companies come in various sizes, from small local companies to large interna-

> *Because [sunflower] is a bee-pollinated crop, sizable isolation distances are required between varieties. Typically 1–1.5 miles [1.8–2.7 km] is utilized.*
>
> (G. Cole, pers. comm., 2005)

tional companies (Duvick, 2004; Fernandez-Cornejo, 2004). The large companies often are units of large international agribusiness corporations that deal in many products other than hybrid seeds. The small companies often supply hybrids to niche markets that are not easily served by the large companies, but they also may compete directly with large companies in large-scale markets such as hybrid maize in the United States of America.

A general pattern in the past has been for small companies to pioneer in development and delivery of hybrids for a given crop, usually with substantial help from public-sector breeders. Then, as the market matures, some of the small companies become very large and self-sufficient. Large agribusiness companies that may want to expand and diversify will purchase other seed companies. At the same time, numerous small seed companies also persist, successfully serving a local clientele.

To some extent this pattern is being followed today in some developing countries (López-Pereira and Morris, 1990). Small local seed companies are formed, or may expand their product line, to produce and sell hybrids adapted to their location; they often depend on public-sector breeders for germplasm in the form of inbred lines and recommended hybrid combinations.

However, the large international seed companies are usually present at the beginning as well (e.g. Hassan, Mekuria and Mwangi, 2001; Rusike, Howard and Maredia, 1997), and sometimes parastastal agencies perform the function of a commercial seed company.

> *Farmers in the state of Bihar, India once showed me some fields of obviously* F_2 *hybrid maize. They had purchased 'hybrid seed' from an itinerant salesman. They assured me that he had better not come around again.*
>
> (D. Duvick, pers. comm., 2005)

> *[Hybrid rice] seeds [in Bangladesh] are distributed through sales representatives of seed companies.*
>
> (H. Miah, pers. comm., 2005)

Evolution of the hybrid seed business in developing countries today does not exactly parallel that of the industrialized countries in earlier decades (e.g. Maredia and Howard, 1998).

11.7 SEED SALES AND DISTRIBUTION

Commercial seed companies employ a variety of ways to sell and distribute their product. Often, a company's local sales representatives will contact the farmers, counsel them on the merits and management needs of the hybrids they hope to sell, and arrange for the sale and delivery of product. In other cases, distributors and retailers of farm products provide similar services, but with more centralized sourcing and less personal contact with the farmer. The smaller and more isolated markets are more likely to be served by distributors/retailers.

11.8 UTILIZATION

11.8.1 Commercial crop production

Commercial producers of both horticultural and field crops will readily plant hybrid cultivars if they outperform the best non-hybrid cultivars, have desired quality traits, and are adapted to the local environment and to the management practices preferred by the producers. The usual caveat applies here, that the breeding of hybrids for farmers' needs must be consistent and

> *CIMMYT [maize] inbreds are used both by commercial (big) seed firms as well as by smaller seed companies in developing countries. The major difference will be that the big multi-nationals … use one of our inbred lines (as such or after further inbreeding and selection) in their hybrids along with a proprietary inbred from their programme, whereas many of the smaller seed firms have directly released [hybrid] combinations [of inbreds] developed and tested by CIMMYT.*
>
> (G. Srinivasan, pers. comm., 2005)

> *In Sudan today, annual acreage of hybrid sorghums has reached one million acres. This successful story of seed production was made possible primarily by a local parastatal, the Sudan Gezira Board.*
>
> (G. Ejeta, pers. comm. 2005

long term; seed supplies must be ample, of good quality and delivered on time; and markets and yield prospects must be sufficiently high that farmers can be assured of ample return on their seasonal investment in hybrid seed.

11.8.2 Home use crop production

In many areas of developing nations, both horticultural and field crops are grown by small-scale farmers for home consumption and may supply most or all of the family's food supply. Often crops are grown for two purposes: to furnish food for the home and also for sale on the market in order to bring in much-needed cash. An additional factor is that small-scale farmers in developing countries often reside in locations with relatively poor agricultural potential, such as on steep mountain slopes or droughty soils, or in unreliable climates. Yield prospects may be low and uncertain. In addition to these problems, these farmers are more likely to be offered relatively low prices for their produce because they are far from the ultimate consumer or have poor transportation to connect them to sources of consumption (e.g. Ekasingh *et al.*, 2004; Ha *et al.*, 2004).

For any of the above reasons, small-scale farmers might conclude that purchase of hybrid seed is a risky investment, a chance they cannot afford to take (Pixley and Bänziger, 2004).

Despite such problems and concerns, small-scale farmers who grow most of their own food have moved strongly to use of hybrid crops in many countries. Size

> *There is no hard and fast rule on consumption and selling of hybrid paddy [in Bangladesh]. Medium [size] farmers prefer consumption if they do not have pressure for selling … for immediate cash money. Big farmers sell most of their products. Commercial production of hybrid rice has no link with farm size. It is the choice of the farmers and the availability of seeds in time.*
>
> (H. Miah, pers. comm., 2005)

> *Some very small farmers buy our [hybrid pepper and tomato] seed, but only if they are able to sell some of the produce to offset the cost of the seed.*
>
> (R. Heisey, pers. comm., 2005)

> *[E]vidence began to accumulate that, despite the conventional wisdom, hybrids in some cases represent an appropriate technology even for small-scale, resource-constrained farmers.*
>
> (López-Pereira and Morris, 1994)

> *Sorghum hybrids are planted by farmers of all sizes. If farmers can recognize value, they will purchase the input … Farm size has little to do with it. Our experience is that farmers will find a way to purchase hybrid seed if it adds value to their operation … They may go together with a neighbour to buy seed and split it or they will make some arrangement for purchasing on credit from the local retailer.*
>
> (K. Porter, pers. comm., 2005)

of farm seems to make no difference, as long as the farmers have reasonably good assurance of favourable growing conditions for the crop and dependable markets if they want to sell some or all of their produce.

Of course small-scale farmers must have some source of cash income in order to pay for the seed, unless they buy it on credit with promise to recompense the seller with some portion of the resulting crop.

But despite a general movement toward use of hybrids for some crops, one must recognize that civil unrest and consequent social and fiscal constraints, or simply lack of well-adapted hybrids, can dictate against purchase and use of hybrid seed. In circumstances such as these, saved seed of non-hybrid cultivars may be the only prudent option.

11.9. PARTICIPATORY PLANT BREEDING FOR HYBRIDS

Breeding systems and the seed production and delivery systems for hybrids are often complicated and require large amounts of labour, capital and genetic expertise.

Farmers cannot easily produce all of these inputs by themselves. And even if farmers could perform all of the steps of hybrid breeding and seed production for themself, the annual cost in terms of land, labour and capital would usually be greater than if the farmers were to simply purchase their hybrid seed for each season's plantings (see Morris and Bellon (2004) for discussion of the trade-offs with participatory plant breeding).

Nevertheless, in certain situations, farmer participation in the hybrid breeding process may be essential or profitable, or both. For example, in some cases neither public nor private plant breeding organizations will have developed hybrids for a particular environmental niche or quality requirement (as noted earlier). In such situations, intensive farmer participation in selection of breeding materials as well as in evaluation trials may help to ensure selection of hybrids that fit the farmers' unique growing conditions, cultural methods or quality preferences. In other cases, local farmers or cooperative organizations, collaborating with public-sector (or private-sector) breeding organizations, may be able to produce and deliver appropriate hybrid seed to an under-served area.

> *An example with hybrid wheat: "Conversion to a sterile cytoplasm and the development of restorers and maintainers would take much time and skill. Use of a chemical hybridizing agent would require access to the chemical, spraying equipment, and also add challenges of timing and efficacy with different genetic backgrounds. Furthermore, the need for large isolated crossing blocks and alternating strips of pollen parent necessary for wheat would use land and resources in small farming communities that might not be able to afford that use of productive land."*
>
> G. Marshall, pers. comm. (2005).

It will be instructive to examine the possibilities for participatory plant breeding at each of the several stages of hybrid breeding and seed production and delivery as discussed earlier. The following comments briefly discuss possibilities for each stage.

Assembling and enriching breeding populations

Professional breeders in public and private breeding programmes are best suited to survey the global supply of useful breeding materials and to assemble appropriate materials for further breeding. However, farmers in developing countries may be best suited to identify and contribute germplasm uniquely adapted to their own environmental or quality requirements, especially if they farm in niche environments or have unique quality needs (see Sperling *et al*., 2001). Professional breeders could use the farmer contributions as key ingredients of new breeding populations intended for use in developing hybrids for those farmers. This method, in a simplified version, was the basis for breeding of hybrids in the industrialized countries when hybrid breeding began in the early years of the twentieth century. Inbred lines were selfed from highly regarded OPCs (e.g. maize breeders in the United States of America selfed favoured farmer varieties such as Reid, Krug and Lancaster); the inbreds were combined into hybrid combinations; and, following evaluation trials, the breeders selected the best hybrids for production and distribution (see Jenkins, 1978).

A caution: in today's environment of intellectual property rights and farmers' rights, proper attention will be needed to ensure that local laws and regulations are obeyed in the process of contribution and use of farmer OPCs (see discussion in Morris and Bellon, 2004).

Inbred line development

Professional breeders are best suited to grow and self-pollinate hundreds or thousands of rows of inbred lines at various stages of inbreeding, rate them for desirable traits, and eventually discard all but a handful of the best new lines. But farmers, if they could spare the land and labour, could provide useful information in a collaborative fashion by growing duplicate rows of the same materials (partially selfed inbreds, *per se*) for observation of performance under their specialized conditions. Breeders could use this information as valuable supplemental information to assist their save or discard decisions in the course of inbreeding.

Farmers, especially poor small-scale farmers in developing countries, would probably not wish to do such collaboration, however, because the inbred lines would use space needed for regular crop production but usually would yield much less than OPCs or hybrids. The farmers' income would be reduced to unacceptable levels. Perhaps the farmers could be paid (in cash or in kind) to perform such a collaborative service.

Professional breeders might be able to justify such an outlay if it added to the speed and precision of their breeding effort. But they too might find the extra effort was not worth the expense except in cases where it was impossible (or too expensive) to reproduce unique abiotic or biotic stresses that occurred in the farm settings.

Also, as noted above, considerations of intellectual property rights might mitigate against such distribution and handling of potentially valuable proprietary germplasm.

Assignment of inbreds to parental groups

Professional breeders, once again, are best suited to perform this operation, using their extensive knowledge of pedigrees, performance of inbred lines in various hybrid combinations, and, increasingly, the information in genomics databases.

Hybrid formation, trials, evaluation

Professional breeders can best organize and carry out these tasks, although farmers can (and should) participate in the evaluation stages. Annually, breeders make many new experimental hybrids, with full knowledge that only a few of them will perform well enough to save and release as acceptable new hybrids. Typically, one must make dozens or hundreds of experimental hybrids for initial observation and yield trials. As noted earlier, a few seasons of performance and evaluation trials in appropriate environments will enable the breeders to reduce the number of experimental hybrids to a much smaller total. This reduced number of hybrids ('advanced experimental hybrids') can then be tested much more widely, in particular in those environments and locations where they are to be grown and used by farmers.

Farmers and breeders can, and do, collaborate in conducting many of these performance trials, especially in the more advanced stages of selection. Such collaboration is common today in industrialized countries, as well as in some regions of developing countries. For example, from the first days of hybrid breeding, seed companies in the United States of America have grown the majority of their advanced small-plot hybrid yield trials on land of collaborating farmers. The professional breeders provide seed, plant the trials and harvest them; the farmers provide land and cultural practices. Sometimes the farmers have received some kind of payment, for example if the trials on average yielded less than the farmer's commercial crop. Breeders use the small-plot information to guide them in evaluating the adaptation of hybrids to particular environments, cultural practices and farmer preferences. Farmer participation is passive in the sense that farmers make no decisions about which hybrids are entered in the trials or which ones are saved, and therefore is one type of Participatory Variety Selection (PVS) (Chapter 3).

Another step in collaborative evaluation in the United States of America came about after farmers adopted combines for harvest, starting in about the 1970s. Experimental hybrids in the final stage of trials are now widely tested by farmers in 'strip trials'. Farmers plant field-length strips (e.g. several rows) of experimental hybrids (often furnished gratis by seed companies) next to strips of their favourite commercial hybrid(s), and at harvest time a measured length of each strip is combine harvested and the grain is weighed, tested for moisture, and yield is calculated. Other notes on pertinent traits may be taken at the same time.

Farmers use these strip-test data (typically those from their own farm and also those from neighbouring farms) to help decide which commercial hybrids to plant in their fields in the following season. Their participation is active in that they choose which hybrids to compare in strip trials and which hybrids to plant in the following season, but is still a type of PVS [Editors' note].

Seed companies use the strip-test data to help them decide which experimental hybrids to save and promote to commercial status (i.e. production and sale) for the following season.

Thousands of such trials are performed each season. Properly analysed, the data can be statistically significant, and can help the breeders to characterize the specific adaptation(s) of each hybrid. They are a valuable addition to the data gathered from traditional small-plot yield trials (for more detail, see Duvick, 2002).

Such collaboration, for small-plot trials or for strip-test trials, can be more difficult to carry out in developing countries, with very different logistics, economies, and farming systems, especially for small-scale farmers. But with appropriate design, organization and supervision, private or public breeders can collaborate with farmers to carry out performance trials of advanced experimental hybrids (see Chapter 9). As in the industrialized countries, the later stages of hybrid selection (when numbers of experimental hybrids are reduced to dozens or fewer, rather than hundreds) will be appropriate for such collaborative trials.

CIMMYT maize breeders have instituted an effective collaborative system of this kind ('Mother-Baby' evaluation trials) in Zimbabwe (Bänziger and de Meyer, 2002). Without unduly taxing farmer land and labour, the system enables selection of hybrids best suited to the local weather, soils and farming methods, educates the farmers in possibilities for hybrid use and value (the trials include OPCs as well as hybrids), and also feeds farmer knowledge and preferences back to the professional breeders.

The two-way interaction, among other things, guides the breeders in selecting appropriate traits and trial conditions for the earlier stages of hybrid breeding and evaluation trials (operations that are performed entirely by the professional breeders). The Mother-Baby trials have produced interesting and useful by-products.

National agricultural research programmes in other southern African countries have adopted versions of the Mother-Baby trials.

> *The Mother Trial was a replicated researcher-managed trial, planted in the centre of a farming community, typically with a school or a progressive farmer. It evaluated 12 cultivars under two input levels, using two-row plots and three replications. Baby Trials were grown by at least six farmers in a community that hosted a Mother Trial. Each Baby Trial contained four of the varieties evaluated in the Mother Trial and all entries in the Mother Trial were represented among Baby Trials. Farmers were requested to treat the four cultivars uniformly but follow their own management practices. … Trial entries came from several public and private breeding programmes chosen by the breeders "as being the best bets for smallholder farmers' conditions". This [method was used] because of the project's goal of exposing farmers to new varieties.*
>
> (Bänziger and de Meyer, 2002)

> *Local farmers and partners suggested that information from Mother-Baby Trials should be made available to retailers to increase the availability of appropriate varieties.*
>
> (Bänziger and de Meyer, 2002).

A less formal but also effective method of participation (used in vegetable breeding) is described below.

Seed production

As noted in the earlier discussion of this topic, the sum total of the logistics, equipment and technical skills required for production and distribution of hybrid seed requires the establishment of formal organizations, and these, typically, have been commercial seed companies. The

> *We do a lot of inbred development and hybrid evaluation in developing countries such as Guatemala and Jordan by working on farms (usually small by our standards) owned and/or run by our dealers and cooperators. We end up with hybrids that are adapted not only for growing by the larger farmers, but also for the marginal farmers*
>
> (R. Heisey, pers. comm., 2005).

seed companies may produce hybrid seed made primarily from inbred lines that are developed by public-sector organizations or that are leased to them by private-sector firms. Alternatively, they may have their own extensive breeding establishment and produce (and primarily depend upon) their own proprietary inbreds and hybrids. Small companies typically follow the first path; larger firms usually take the second route.

There is a third possibility. Farmers can form cooperatives to produce hybrid seed for themselves; they can use inbreds from the public sector in approximately the same way as is done by the smaller commercial firms. Although cooperatives come in various forms, one can use the definition: ‘a jointly owned commercial enterprise (usually organized by farmers or consumers) that produces and distributes goods and services and is run for the benefit of its owners.’ Thus, although the members of the cooperative would control its activities and share in its benefits, the cooperative also would be a commercial company in the sense that it would market seed to farmers.

A drawback to formation of cooperatives for hybrid seed production and distribution is that substantial amounts of capital and skilled personnel would be required. Training in hybrid seed production might come from public-sector organizations (or appropriate NGOs) and loans of capital might be arranged through suitable government organizations. But these requirements in capital and training of personnel could be significant or even impossible obstacles for poor farmers in countries or regions with unstable government and economy.

A second important consideration is that the seed production cooperative would need continuing services, through the years, of a public-sector organization to develop inbreds and hybrid combinations. The public-sector establishment would need to provide a constant flow of new inbreds and hybrids to keep up with changing disease and insect problems, and perhaps changing abiotic challenges as well. This assumes that the cooperative would not do its own breeding, or contract with the private sector for such materials. Without such a source of inbreds and hybrids, there would be no justification for forming a cooperative.

An experienced sorghum breeder has given a concise summary of requirements for a hybrid seed production cooperative as follows:

Farmer-organized hybrid seed companies were formed in the United States of America in the early days of hybrid breeding. For example, Dr H.C.M. Case (professor at the University of Illinois) and five farmers from Champaign County, Illinois, organized the Champaign County Seed Company, in 1937 (Widick, 2005). The organization was formed to ‘grow, condition and sell hybrid maize seed’ as one of the ‘associated growers’ of Lester Pfister. Pfister was an entrepreneurial farmer-breeder of maize hybrids who had enlarged the seed production and sale capacity of his company (the Pfister Hybrid Corn Company) by forming Pfister Associated

> *Cooperatives can produce their own seed if they are willing to invest in the seed production elements that result in quality seed. These are: (1) a mechanism to ensure getting pure seed of inbred parents; (2) training of qualified seed plant managers; (3) identification of reliable farmer seed growers; (4) hiring people to manage the various aspects of seed production (planting dates to ensure isolation, removing rogues, proper harvest techniques, etc.); (5) acquiring facilities for drying and conditioning the seed for maximum quality; (6) evaluation of final quality (germination, vigour test, purity, etc.); (7) proper packaging; and (8) storage facilities.*
>
> (K. Porter, pers. comm., 2005)

Growers (P.A.G.), consisting of approximately two dozen independent seed production enterprises like the Champaign County Seed Company. P.A.G. eventually reorganized as an independent, relatively large-scale conventional seed company with its own breeding programme. In due course, an even larger company purchased P.A.G. (Fernandez-Cornejo, 2004).

Despite the potential difficulties discussed in previous paragraphs, farmer cooperatives have been formed in developing countries to produce hybrid seed.

The Philippine cooperatives appear to be transitioning into small seed companies that depend on public-sector breeders for inbreds and hybrids.

A different way for farmers to participate in (and profit from) hybrid seed production is to produce hybrid seed on their farms, on contract to commercial seed firms. In India, hundreds of farmers in Andhra Pradesh produce hybrid maize seed in this way, guided and trained by a local contractor, or by the seed companies directly. The seed production is said to be economical and of high quality. The farmers are compensated on the basis of the amount of seed they produce for the contracting company. This enterprise ‘is a huge source of income and contribution to the local economy’ (G. Srinivasan and D. Beck, pers. comm., 2005).

> *Farmers’ cooperatives in Viet Nam have played a role in the hybrid rice seed industry for some time now. The seeds harvested are turned over to the provincial seed companies that in turn sell the seeds to the farmers. There are now nine community-based farmers’ cooperatives for hybrid rice seed production in the Philippines. They mainly produce seed of the public-sector-developed hybrids. The national research institute provides technical backstopping whenever needed by the cooperatives. The Philippine Rice Research Institute, which is responsible for the development and dissemination of the technology, facilitated the establishment of these cooperatives. It was responsible for the development and dissemination of the technology. In the beginning, seeds produced by the cooperatives were procured by the government and sold to the farmers at subsidized prices. The subsidy is now gradually being phased out and the marketing of the hybrid seeds is transferred entirely to the cooperatives. The sustainability of this arrangement remains to be seen since seed marketing has been only recently transferred to the cooperatives*
>
> (R.S. Toledo, pers. comm., 2005)

Seed sales and distribution

As noted above, cooperatives might not only produce hybrid seed, they might distribute it as well. To maximize the profitability of their investment in production facilities and trained personnel, they might choose to sell to a broader market than only the members. At this point, it would be hard to distinguish the cooperatives from traditional small seed companies.

General comments in regard to participatory plant breeding for hybrids

Farmers have fewer opportunities to collaborate with professional breeders in the several stages of the hybrid breeding, production and distribution process than is possible for breeding of non-hybrid cultivars. Possibilities for farmer participation are primarily in hybrid evaluation and, to some degree, in seed production and distribution (e.g. farmer cooperatives or contract seed production).

The use of cooperatives for seed production and distribution requires (i) formation of a well-managed corps of skilled operators; (ii) meticulous and sometimes difficult hybridization operations; and (iii) well organized and often expensive facilities and distribution systems. This complicated seed production and distribution step is not needed, or can be done more simply, in participatory breeding of non-hybrid crops, e.g. in production of farmer-saved seed. Seed production and distribution of hybrids is best performed by organized business entities.

Nevertheless, when all is said and done, the facts are that individual farmers can and do participate constructively in some of the stages of hybrid breeding, production and distribution. In so doing they help themselves—they help to ensure the availability of hybrids that suit their needs and financial status.

In the absence of a viable seed industry, the means to get hybrid [sorghum] seed produced and marketed will, I believe, have to come from within the farm community. [But] seed production is a vital knowledge and experience that needs to be built up.

(G. Ejeta, pers. comm., 2005)

Each crop is different. The farmer/breeders will need a great deal of assistance on many things … producing, harvesting, processing, and marketing the seed.

(W. Meredith, pers. comm., 2005)

[The] Bangladesh perspective, in limited scale, is to invite farmers in at several stages of plant growth to watch the hybrid fields managed by plant breeders. Farmers are at liberty to give their opinions … and breeders seriously consider them in their further course of action. … For seed production, one NGO (Rangpur Dinajpur Rural Service) organized women farmers who were trained in the Bangladesh Rice Research Institute. These groups of women farmers did a marvellous job in producing quality seeds.

(H. Miah, pers. comm., 2005)

We find that farmers (even small-acreage farmers) are very interested in helping with the research programmes by providing land for growing breeding nurseries or screening nurseries. They are anxious to assist with hybrid testing and evaluation and provide excellent input on specific traits that impact their profitability. They also provide excellent input and comments as we visit with them during crop tours and research trial visits.

(K. Porter, pers. comm., 2005)

11.10. CONCLUSIONS

Breeding and use of hybrid cultivars has increased worldwide and in significant amount during the past several decades, in part because of continuing development of effective and economic systems for hybrid seed production and in part because of continuing genetic improvements in performance and profitability of the hybrids (e.g. Axtell *et al.*, 1999; Duvick, 2005; López-Pereira and Morris, 1990). Hybrids work for many crops, but not all; they work in many farming regions of the world but not all farming regions; and they work for many farmers, but not all farmers.

It seems likely that in the years to come, hybrid development, distribution and utilization in all parts of the world will depend primarily on effective services of a diverse array of private seed companies. Some companies will carry out the entire spectrum of breeding and evaluation, seed production, and delivery, while others, such as smaller companies and farmer cooperatives, will depend to a greater or lesser degree on inbred lines and improved germplasm from the public sector (or, at times, leased from other companies in the private sector). In addition to the ongoing need for public-sector breeding of inbreds and hybrids, there will be a continuing need for the fundamental products—both germplasm and knowledge—that are provided by able public-sector professional plant breeders. Public-sector contributions will be especially important for development and provision of hybrids to small-scale farmers in some of the disadvantaged farming regions of developing countries.

Farmers will participate in hybrid breeding. Their participatory plant breeding activities will be essential and beneficial to farmers and breeders alike, but farmer participation will be less than is feasible in breeding of non-hybrid cultivars.

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REFERENCES

Anagnostakis, S.L. 2005. Chestnuts and the introduction of Chestnut Blight (available at http://www.caes.state.ct.us/FactSheetFiles/PlantPathology/fspp008f.htm).

Anonymous. 2005. Hybrid Cotton (available at http://www.ikisan.com/links/ap_cotton-Hybrid%20Cotton.shtml).

Arias, D.M. & Rieseberg, L.H. 1995. Genetic relationships among domesticated and wild sunflowers (*Helianthus annuus*, Asteraceae). *Economic Botany,* 49: 239–248.

Axtell, J., Kapran, I., Ibrahim, Y., Ejeta, G. & Andrews, D.J. 1999. Heterosis in sorghum and pearl millet. *In* J.G. Coors & S. Pandey, eds. *Genetics and exploitation of heterosis in crops.* pp. 375–386. Madison, USA, ASA/CSSA/SSSA.

Bänziger, M. & de Meyer, J. 2002. Collaborative maize variety development for stress-prone environments in southern Africa. *In* D.A. Cleveland & D. Soleri, eds. *Farmers, scientists and plant breeding: integrating knowledge and practice,* pp. 269–296. Wallingford, UK, CABI.

Bänziger, M., Edmeades, G.O. & Lafitte, H.R. 1999. Selection for drought tolerance increases maize yields across a range of nitrogen levels. *Crop Science,* 39: 1035–1040.

Bänziger, M., Setimela, P.S., Hodson, D. & Vivek, B. 2004. Breeding for improved abiotic stress tolerance in maize adapted to southern Africa. *In* T. Fischer *et al*., eds. *New directions for a diverse planet.* Proceedings of the 4th International Crop Science Congress, Brisbane, Australia, 26 September–1 October 2004. The Regional Institute Ltd., Gosford, Australia.

Bi, X., de Palma, J., Oane, R., Khush, G.S. & Benett, J. 2003. Molecular approaches for fixing the heterozygosity of hybrid rice. *In* S.S. Virmani *et al.*, eds. *Hybrid rice for food security, poverty alleviation, and environmental protection,* pp. 135–150. Proceedings of the 4th International Symposium on Hybrid Rice, Hanoi, Viet Nam, 14–17 May 2002. Los Baños, Philippines, IRRI.

Brown, G.G. 1999. Unique aspects of cytoplasmic male sterility and fertility restoration in *Brassica napus*. *Journal of Heredity,* 90: 351–356.

Butler, L.J. & Marion, B.W. 1985. The impacts of patent protection on the U.S. seed industry and public plant breeding. NC Regional Research Publication No. 304. University of Wisconsin-Madison, Madison, USA. 128 p.

Canola Advantage. 2005. *Growing canola* (available at http://www.canola-council.org/hybridssyntheticcanola.aspx).

J.G. Coors & Pandey, S., eds. 1999. *Genetics and exploitation of heterosis in crops.* Madison, USA, ASA/CSSA/SSSA.

Crabb, R. 1993. *The hybrid corn-makers.* 2nd ed. West Chicago, USA, West Chicago Publishing Company. 414 p.

Ding, D., Gai, J., Cui, Z. & Qiu, J. 2002. Development of a cytoplasmic-nuclear male-sterile line of soybean. *Euphytica,* 124: 85–91.

Duvick, D.N. 1966. Influence of morphology and sterility on breeding methodology. *In* K.J. Frey, ed. *Plant breeding,* pp. 85–138. Ames, USA, Iowa State University Press.

Duvick, D.N. 1984. Genetic diversity in major farm crops on the farm and in reserve. *Economic Botany,* 38: 161–178.

Duvick, D.N. 1997. What is yield? *In* G.O. Edmeades *et al*., eds. *Developing drought- and low N-tolerant maize,* pp. 332–335. Proceedings of a Symposium, CIMMYT, El Batan, Mexico, 25–29 March 1996., México, D.F., CIMMYT.

Duvick, D.N. 2002. Theory, empiricism and intuition in professional plant breeding. *In* D.A. Cleveland & D. Soleri, eds. *Farmers, scientists and plant breeding: Integrating knowledge and practice*. pp. 189–211. Wallingford, UK, CABI Publishing.

Duvick, D.N. 2004. Keynote 2 – The current state of plant breeding: How did we get here? *In* M. Sligh & L. Lauffer, eds. *Summit Proceedings: Summit on Seeds and Breeds for 21st Century Agriculture,* pp. 71–91. Washington, DC, Pittsboro, USA, Rural Advancement Foundation International-USA.

Duvick, D.N. 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). *Advances in Agronomy,* 86: 83–145.

Duvick, D.N., Smith, J.S.C. & Cooper, M. 2004. Long-term selection in a commercial hybrid maize breeding program. *In* J. Janick, ed. *Plant Breeding Reviews, Part 2, Long-term selection: crops, animals, and bacteria,* pp. 109–151. Vol. 24.

Edmeades, G.O., Bänziger, M. & Cortes-C., M. 1997. From stress-tolerant populations to hybrids: The role of source germplasm. *In* G.O. Edmeades *et al*., eds. *Developing drought- and low N-tolerant maize,* pp. 263–272. Proceedings of a Symposium, CIMMYT, El Batan, Mexico, 25–29 March 1996. México D.F., CIMMYT.

Ejeta, G. 1988. Development and spread of Hageen Dura-1, the first commercial sorghum hybrid in the Sudan. *Applied Agricultural Research,* 3: 29–35.

Ekasingh, B., Gypmantasiri, P., Thongngam, K. & Grudloyma, P. 2004. *Maize in Thailand: Production systems, constraints, and research priorities.* Mexico, D.F., CIMMYT. 36 p.

ERS [Economic Research Service, USDA]. 2004. *Agricultural biotechnology intellectual property* (available at http://www.ers.usda.gov/Data/AgBiotechIP/).

Fernandez-Cornejo, J. 2004. The seed industry in U.S. agriculture: An exploration of data and information on crop seed markets, regulation, industry structure, and research and development. Bulletin 786. USDA-ERS, Washington, DC.

French, D.W., Ascerno, M.E. & Stienstra, W.C. 1980. *The Dutch Elm disease.* AG-BU-0518. Minnesota Extension Service, University of Minnesota, St. Paul, USA.

Geiger, H.H. & Miedaner, T. 1999. Hybrid rye and heterosis. *In* J.G. Coors & S. Pandey, eds. *Genetics and exploitation of heterosis in crops,* pp. 439–450. Madison, USA, ASA/CSSA/SSSA.

Grando, S., von Bothmer, R. & Ceccarelli, S. 2001. Genetic diversity of barley: use of locally adapted germplasm to enhance yield and yield stability of barley in dry areas. *In* H.D. Cooper, C. Spillane & T. Hodgkin, eds. *Broadening the Genetic Base of Crop Production*, pp. 351-372. New York, USA, CABI/Rome, FAO/Rome, IPGRI.

Guohui, M. & Longping, Y. 2003. Hybrid rice achievements and development in China. *In* S.S. Virmani *et al.*, eds. *Hybrid rice for food security, poverty alleviation, and environmental protection,* pp. 247–256. Proceedings of the 4th International Symposium on Hybrid Rice, Hanoi, Viet Nam, 14–17 May 2002. Los Baños, Philippines, IRRI.

Ha, D.T., Thao, T.D., Khiem, N.T., Trieu, M.X., Gerpacio, R.V. & Pingali, P.L. 2004. *Maize in Vietnam: Production systems, constraints, and research priorities.* Mexico, D.F., CIMMYT. 42 p.

Hanna, W.W. 1995. Use of apomixis in cultivar development. *Advances in Agronomy,* 54: 333–350.

Hassan, R.M., Mekuria, M. & Mwangi, W. 2001. Maize breeding research in eastern and southern Africa: Current status and impacts of past investments made by the public and private sectors 1966–97. Mexico, D.F., CIMMYT. 33 p.

Haussmann, B.I.G., Obilana, A.B., Ayiecho, P.O., Blum, A., Schipprack, W. & Geiger, H.H. 2000. Yield and yield stability of four population types of grain sorghum in a semi-arid area of Kenya. *Crop Science,* 40: 319–329.

Heisey, P.W., Rubenstein, K.D. & King, J.L. 2005. Patterns of public and private sector patenting in agricultural biotechnology. *AgBioForum* 8(2-3): 73–82 (available at www.agbioforum.org; accessed 31 Jan. 2009).

Ilagan, L. 2004. Hybrid rice seed 'cheats' revealed. *The Manila Times,* 17 August 2004. Manila.

Iowa State Department of Agriculture. 1934. Part VI. Iowa Corn and Small Grain Growers' Association *Thirty-fifth annual Iowa year book of agriculture,* pp. 135–148. Iowa State Department of Agriculture, Des Moines, USA.

James, C. 2002. *Global review of commercialized transgenic crops. 2001 Feature: Bt cotton*. Ithaca, USA, ISAAA.

Janick, J. 1998. Hybrids in horticultural crops. *In* K.R. Lamkey & J.E. Staub, eds. *Concepts and breeding of heterosis in crop plants: Special publication number 25*, pp. 45–56. Madison, USA, CSSA.

Jenkins, M.T. 1978. Maize breeding during the development and early years of hybrid maize. *In* D.B. Walden, ed. *Maize breeding and genetics*, pp. 13–28. New York, USA, John Wiley and Sons.

Jones, D.F. 1918. *The effects of inbreeding and cross-breeding upon development*. Connecticut Agricultural Experiment Station, New Haven, USA.

Jones, D.F. 1922. The productiveness of single and double first generation corn hybrids. *Journal of the American Society of Agronomy,* 14: 241–252.

Jordaan, J.P., Engelbrecht, S.A., Malan, J.H. & Knobel, H.A. 1999. Wheat and heterosis. *In* J.G. Coors & S. Pandey, eds. *Genetics and exploitation of heterosis in crops,* pp. 411–421. Madison, USA, ASA/CSSA/SSSA.

Joshi, P.K., Singh, N.P., Singh, N.N., Gerpacio, R.V. & Pingali, P.L. 2005. *Maize in India: Production systems, constraints, and research priorities.*, Mexico, D.F., CIMMYT. 42 p.

Knudson, M.K., & Ruttan, V.W. 1988. The R&D of a biological innovation: The case of hybrid wheat. *Food Research Institute Studies,* 21: 45–67.

Koemel, J.E. Jr, Guenzi, A.C., Carver, B.F., Payton, M.E., Morgan, G.H. & Smith, E.L. 2004. Hybrid and pureline hard winter wheat yield and stability. *Crop Science,* 44: 107–113.

Kunz, K., ed. 2002. *Vegetable breeding for market development.* Bangkok, East West Seed International Ltd. 150 p.

Large, E.C. 1962. *The advance of the fungi.* New York, USA, Dover Publications. 488 p.

López-Pereira, M.A. & Morris, M.L. 1990. Impacts of international maize breeding research in the developing world, 1966–1990. México D.F., CIMMYT. 58 p.

Maredia, M. & Howard, J. 1998. *Facilitating seed sector transformation in Africa: Key findings from the literature.* USAID - Bureau for Africa, Office of Sustainable Development, Washington, DC.

Matossian, M.K. 1989. *Poisons of the past: Molds, epidemics, and history.* New Haven, USA, and London, Yale University Press. 190 p.

Melchinger, A.E. & Gumber, R.K.. 1998. Overview of heterosis and heterotic groups in agronomic crops. *In* K.R. Lamkey & J.E. Staub, eds. *Concepts and breeding of heterosis in crop plants: Special publication number 25*, pp. 29–44. Madison, USA, CSSA.

Menkir, A. & Akintude, A.O. 2001. Evaluation of the performance of maize hybrids, improved open-pollinated and farmers' local varieties under well-watered and drought stress conditions. *Maydica,* 46: 227–238.

Meredith, W.R. Jr. 1999. Cotton and heterosis. *In* J.G. Coors & S. Pandey, eds. *Genetics and exploitation of heterosis in crops,* pp. 451–462. Madison, USA, ASA/CSSA/SSSA.

Miller, J.F. 1987. Sunflower. *In* W.R. Fehr, ed. *Principles of cultivar development*. pp. 626–668. New York, USA, Macmillan Publishing Company.

Mojayad, F. & Planchon, C. 1994. Stomatal and photosynthetic adjustment to water deficit as the expression of heterosis in sunflower. *Crop Science,* 34: 103–107.

Morris, M.L. & Bellon, M.R. 2004. Participatory plant breeding research: Opportunities and challenges for the international crop improvement system. *Euphytica,* 136: 21–35.

NRC [National Research Council]. 1972. *Genetic vulnerability of major crops.* Report of the National Research Council Committee on Genetic Vulnerability of Major Crops. Washington, DC, National Academy of Sciences. 307 p.

Nicolas, D. 2005. Blés hybrides: les ventes progressent doucement. *Agro Performances,* April: 32–33.

Owen, F.V. 1945. Cytoplasmically inherited male-sterility in sugar beets. *Journal of Agricultural Research,* 71: 423–440.

Palmer, R.G., Gai, J., Sun, H. & Burton, J.W. 2001. Production and evaluation of hybrid soybean. *Plant Breeding Reviews,* 21: 263–307.

Paudyal, K.R., Ransom, J.K., Rajbhandari, N.P., Adhikari, K., Gerpacio, R.V. & Pingali, P.L. 2001. *Maize in Nepal: Production systems, constraints, and priorities for research.* NARC and CIMMYT, Kathmandu. 48 p.

Perotti, E., Grimanelli, D., John, P., Hoisington, D. & Leblanc, O. 2004. Why is transferring apomixis to crops still a dream? *In* T. Fischer *et al*., eds. *New directions for a diverse planet.* Proceedings of the 4th International Crop Science Congress, Brisbane, Australia, 26 September–1 October 2004. The Regional Institute Ltd., Gosford, Australia.

Pixley, K. & Bänziger, M. 2004. Open-pollinated maize varieties: A backward step or valuable option for farmers? *In* D.K. Friesen & A.F.E. Palmer, eds. *Integrated approaches to higher maize productivity in the New Millennium*, pp. 22–28. Proceedings of the 7th Eastern and Southern Africa Regional Maize Conference, Nairobi, Kenya, 5-11 February 2002. CIMMYT and KARI (Kenya Agricultural Research Institute)., Mexico, D.F., CIMMYT.

Pons, L. 2003. Heart-friendly corn oil? New high-oleic corn varieties make it possible. *Agricultural Research Magazine (USDA-ARS),* 51: 18–19.

Rajaram, S., Singh, R.P. & Ginkel, M.V. 1997. Breeding wheat for wide adaptation, rust resistance and drought tolerance. In *Crop Improvement for the 21st Century*, pp. 139–163. Trivandrum, India, Research Signpost.

Renard, M., Delourme, R., Vallée, P. & Pierre, J. 1998. Hybrid rapeseed breeding and production. *In* G. Thomas & A. Monteiro, eds. Proceedings of the International Symposium on Brassicas. *Acta Horticulturae,* 459: 291–298.

Rick, C.M. & Chetelat, R.T. 1995. Utilization of related wild species for tomato improvement. *Acta Horticulturae,* 412: 21–38.

Roberts, A. 2005. Hazera no longer novelty, gaining more attention (available at http://westernfarmpress.com/mag/farming_hazera_no_longer/index.html).

Rusike, J., Howard, J. & Maredia, M. 1997. Seed sector evolution in Zambia and Zimbabwe; Has farmer access improved following economic reform? *Policy Synthesis for USAID - Bureau for Africa, Office of Sustainable Development* 31: 1-4.

Saaten-Union. 2005. Le site du blé hybride (available at http://www.blehybride.com/).

Seiler, G.J. 1992. Utilization of wild sunflower species for the improvement of cultivated sunflower. *Field Crops Research,* 30: 195–230.

Simmonds, N.W. 1993. Introgression and incorporation – Strategies for the use of crop genetic resources. *Biological Reviews of the Cambridge Philosophical Society,* 68(4): 539–562.

Simon, P.W. 2000. Domestication, historical development, and modern breeding of carrot. *Plant Breeding Reviews,* 19: 158–190.

Smale, M., Reynolds, M.P., Warburton, M., Skovmand, B., Trethowan, R., Singh, R.P., Ortiz-Monasterio, I. & Crossa, J. 2002. Dimensions of diversity in modern spring bread wheat in developing countries from 1965. *Crop Science,* 42: 1766–1779.

Smith, M.B., Horner, H.T. & Palmer, R.G. 2001. Temperature and photoperiod effects on sterility in a cytoplasmic male-sterile soybean. *Crop Science,* 41: 702–704.

Sperling, L., Ashby, J.A., Smith, M.E., Weltzien, E. & McGuire, S. 2001. A framework for analyzing participatory plant breeding approaches and results. *Euphytica,* 122: 439–450.

Stephens, J.C. & Holland, R.F. 1954. Cytoplasmic male-sterility for hybrid sorghum seed production. *Agronomy Journal,* 46: 20–23.

Swastika, D.K.S., Kasim, F., Sudana, W., Hendayana, R., Suhariyanto, K., Gerpacio, R.V. & Pingali, P.L. 2004. *Maize in Indonesia: Production systems, constraints, and research priorities.* Mexico, D.F., CIMMYT. 40 p.

Tanksley, S.D., Grandillo, S., Fulton, T.M., Zamir, D., Eshed, Y., Petiard, V., Lopez, J. & Beck-Bunn, T. 1996. Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. pimpinellifolium*. *Theoretical and Applied Genetics,* 92: 213–224.

Tatum, L.A. 1971. The southern corn leaf blight epidemic. *Science,* 171: 1113–1116.

Tollenaar, M. & Wu, J. 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. *Crop Science,* 39: 1597–1604.

Tracy, W.F. & Chandler, M.A. 2004. The historical and biological bases of the concept of heterotic patterns in Corn Belt Dent maize. Annual Corn & Sorghum Research Conference Proceedings, 8–10 December 2004. Audio CD. American Seed Trade Association. Alexandria, USA.

University System of Maryland. 2004. Bylaw IV – 3.20. University System of Maryland Policy on Intellectual Property (Approved by the Board of Regents, February 8, 2002; amended by the Chancellor, July 7, 2004) (available at http://www.usmd.edu/Leadership/BoardOfRegents/Bylaws/SectionIV/IV320.html).

USDA-NASS. 2000. Crops Production Data, by States, 1866-1997. USDA-National Agricultural Statistical Service, Washington, DC.

Van der Plank, J.E. 1963. *Plant diseases: Epidemics and control.* New York, USA, Academic Press. 349 p.

Virmani, S.S., ed. 1994. *Hybrid rice technology: New developments and future prospects. Selected papers from the International Rice Research Conference.* Los Baños, Laguna, Philippines, IRRI. 296 p.

Virmani, S.S. & Kumar, I. 2004. Development and use of hybrid rice technology to increase rice productivity in the tropics. *International Rice Research Notes* 29.1/2004. Manila, IRRI.

Virmani, S.S., Mao, C.X. & Hardy, R., eds. 2003. *Hybrid rice for food security, poverty alleviation, and environmental protection.* Los Baños, Philippines, IRRI. 407 p.

Wehner, T.C. 1999. Heterosis in vegetable crops. *In* J.G. Coors & S. Pandey, eds. *Genetics and exploitation of heterosis in crops,* pp. 387–397. Madison, USA, ASA/CSSA/SSSA.

Whitt, S.R., Wilson, L.M., TenaiIlon, M.I., Gaut, B.S. & Buckler IV, E.S. 2002. Genetic diversity and selection in the maize starch pathway. *Proceedings of the National Academy of Sciences of the USA,* 99: 12959–12962.

Widick, J. 2005. Company history: PAG hybrids, GSC hybrids (available at http://www.sunprairieseeds.com/history2.htm).

Yuan, L.P. 1998. Hybrid rice development and use: innovative approach and challenges (available at http://www.fao.org//DOCREP/003/W8595T/w8595t02.htm).

Yuan, L.P., Yang, Z.Y. & Yang, J.B. 1994. Hybrid rice research in China. *In* S.S. Virmani *et al.*, eds. *Hybrid rice for food security, poverty alleviation, and environmental protection,* pp. 143–147. Proceedings of the 4th International Symposium on Hybrid Rice, Hanoi, Viet Nam, 14–17 May 2002. Los Baños, Philippines, IRRI.

CHAPTER 12

Selection methods Part 4: Developing open-pollinated varieties using recurrent selection methods

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12.1 INTRODUCTION

This chapter provides an overview of the use of recurrent population improvement methods in variety development. The major stages of population improvement are addressed, from setting objectives and population creation, through progeny development and selection, to recombination. Factors contributing to successful use of recurrent population improvement methods for participatory variety development are provided, and examples given of farmers' contributions to these efforts.

12.2 RECURRENT SELECTION: WHAT IS IT AND HOW DOES IT CONTRIBUTE TO VARIETY DEVELOPMENT?

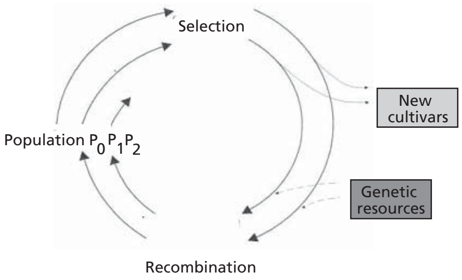
Recurrent selection schemes involve cycles of testing, selection and recombination of breeding 'units', with the possibility of deriving new varieties from each population cycle bulk or from the progenies developed during each cycle (Figure 12.1). Repeated cycles of selection are conducted to increase the frequency of desirable alleles in a population, and obtain progenies that are superior to the best progenies of the previous cycle (Figure 12.2). Ideally, the genetic variability in the population is maintained and thus further genetic gains can be achieved in subsequent cycles.

Recurrent selection methods are readily applied in out-crossing species, where ease of crossing facilitates the frequent and extensive recombinations required in these schemes. The extensive crossing can be more laborious in self-pollinating crops, and requires committed efforts for extensive emasculated crossing or the employment of male-sterility genes or selection for higher out-crossing rates to facilitate recombination.

The basic scheme of recurrent selection is presented in Figure 12.3, with terminology proposed by Strahwald and Geiger (1988). The plants or progenies that are selected to constitute the next, hopefully improved, population bulk are termed selection units. Selection is based on the performance of individual plants or progenies, named evaluation units, for a single trait or an index of several traits. The next cycle of the population is created by inter-mating the selected plants or progenies which are called the recombination units. These different

FIGURE 12.1

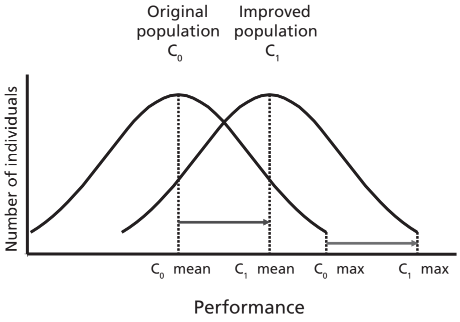
Schematic presentation of an open recurrent selection scheme with cyclic selection and recombination combined with introgression of new germplasm



Becker, 1993.

FIGURE 12.2

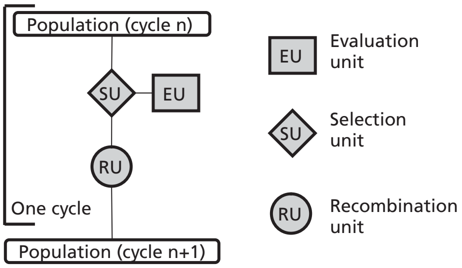
Expected performance distribution of progenies from the original and an improved population



After Fehr, 1987.

FIGURE 12.3

Generalized population improvement scheme for advancing a population from one cycle to the next



From Strahwald and Geiger, 1988.

units are related to one another or may even be identical, depending on the selection method used. For example, in simple mass selection in a highly cross-pollinating species, the selected S_0 plants are the evaluation and selection units as well as the recombination units, with the half-sib seed of the selected plants used to produce the next cycle bulk. A more complicated example would be an S_2 population improvement scheme where S_2 progeny bulks are used as the evaluation units in order to have sufficient seed for multi-environment testing. The selection units and recombination units in this case could be the original S_1 progenies, when remnant S_1 seed of the superior S_2 bulks is used for recombination.

A wide range of recurrent selection methods are available, with alternative methods normally identified by the progeny type used as the test unit (Table 12.1), (Hallauer and Miranda, 1981; Gallais, 1981). The choice of selection scheme depends on the type of end-product desired (improved population or pure-line varieties) and the traits to be improved. It also depends on the crop species to be improved (autogamous or allogamous) and the resources and costs (e.g. labour, test site facilities) the breeder can apply for the recurrent selection. For example, the development of pure-line varieties with high grain yield performance could be more successfully pursued by S_1 or S_2 selection methods using multi-location testing of a very large number of test units that more closely resemble the desired end product. In contrast, the development of more genetically heterogeneous varieties of an allogamous species could well be

TABLE 12.1

Alternative recurrent selection methods, required number of generations (or years), and degree of exploitation of the variance of additive (σ_A^2) and dominance (σ_D^2) effects

Selection method	**Generations per cycle**	**Genetic variance σ_G^2**	
		σ_A^2	σ_D^2
Phenotypic (mass)(1) With recombination			
One sex (after flowering)	1	1/2	1
Both sexes (before flowering)	1	1	1
Half-sib			
Selfs recombined	2	1/2	0
Half-sibs recombined	2	1/4	0
Full-sib	2	1/2	1/4
S_1-line	3	1(1)	1/4(2)
S_2-line	4	3/2(1)	3/16(2)

Notes: (1) Not equal to σ_A^2 unless p = q = 0.5 and dominance decreases to zero with inbreeding.
(2) Coefficient difficult to define unless p = q = 0.5.
Source: adapted from Schipprack, 1993.

done by applying mass selection for simply inherited traits.

The genetic diversity that is retained in the improved populations enables continued improvement. Several cycles of directional selection should increase the frequency of desirable alleles, resulting in higher probabilities of obtaining superior progenies than in the original population (Figure 12.2). Furthermore, the genetic variability retained in a broad-based population enables selection for different traits or adaptation to new target conditions as the needs emerge. Examples of this are listed below.

- A broad-based population retaining substantial diversity for maturity or other adaptive traits could be given to breeders (researchers or farmers) in differing agro-ecological zones, to develop zone-specific populations.
- A population retaining variability for grain quality traits could be used to derive distinct populations for other quality requirements.
- Rare dwarf segregants in a tall-plant-height population can be selected to develop a new short-plant-height population with potential for increased grain harvest index.

12.3 EXPECTED GENETIC GAIN OR THE RESPONSE TO SELECTION

The response to selection (R), using any type of selection, is a function of the intensity of selection (i), the extent to which observed differences are determined by genetic causes (h = square root of heritability) and the extent of additive genetic variation (σ_A), as indicated by the formula (Falconer, 1981):

$$R = i^* h^* \sigma_A$$

The different recurrent selection methods listed in Table 12.1 vary fundamentally for the degree to which they can exploit the available additive genetic variance (σ_A). The other two factors (selection intensity and heritability) can be managed by breeders to optimize genetic gains. Options for managing these factors will be discussed in more detail in the sections on mass- and progeny-based selection methods.

It is crucial to consider the time to complete a cycle of selection since the amount of progress is determined both by the gain per cycle and the time per cycle. Table 12.1 indicates the minimum number of generations required for various methods. The time required for one cycle can be reduced significantly if off-season nursery facilities are available.

12.4 BREEDING OPEN-POLLINATED VARIETIES USING RECURRENT SELECTION METHODS

Varieties of cross-pollinated species can be developed by selection in a population bulk *per se.* This approach is appropriate where intra-varietal heterogeneity is desirable or necessary. Varieties can be derived from the population bulk *per se* by mass selection for specific highly heritable traits that give the variety a more distinct character; for example, a narrower range of flowering dates or more uniform plant height, or grain or plant colour. The highly successful pearl millet variety ICMV 155 was created by this method, with 59 S_0 plants mass selected during the random mating of the New Elite Composite Cycle 4 bulk used to create a new variety (Singh *et al.*, 1994).

Varieties of cross-pollinated species can also be developed from a set of superior progenies identified during the selection phase of progeny-based recurrent selection. For each variety, a separate set of progenies would be identified based on a distinct selection criterion or combination of traits, and the progenies in this set would be recombined to create the new variety. Several different varieties can be created in this manner from a given set of population progenies by selecting for different trait combinations or placing different emphasis (weighting) on the targeted traits. Examples of successful pearl millet varieties developed in this manner are ICTP 8203, created by random mating 5 superior S_2-lines identified by progeny testing a large number of lines derived from a Togolese landrace at Patancheru, India (Rai *et al.,* 1990), and WC-C75, created from 7 full-sib progenies selected out of the World Composite (Andrews, Gupta and Singh, 1985).

Pure-line varieties for predominantly self-pollinating crop species such as sorghum can be effectively derived from the superior partially inbred evaluation units (for example S_1 or S_2 lines) identified in a progeny-based recurrent selection programme. Breeders usually follow the same procedures as for deriving lines from bi-parental crosses (Chapter 11, this volume).

Use of recurrent selection methods in variety development programmes can be particularly advantageous for enhancing quantitative traits determined by many genes, or simultaneous enhancement of multiple traits. A large number of favourable alleles can be carried forward and concentrated with repeated recombination, breaking undesirable linkages, and selection for favourable recombinants. Allard (1999) notes that the assembly of favourable epistatic combinations of alleles of different loci by means of recurring cycles of selection and intercrossing the superior selections is the single most important genetic mechanism for evolution of adaptation.

12.5 SETTING GOALS AND DEVELOPING BASE POPULATIONS

The success of any plant breeding programme is usually measured by the extent of farmer adoption of the newly produced varieties. As the specific advantages of new varieties determine adoption, breeders must tailor their new varieties to meet priority needs and requirements of the end users. Priority setting for a recurrent selection programme requires good understanding of the environmental conditions under which the newly developed varieties should perform, as well as of the needs of the farmers or end users expected to benefit from the new varieties. Methods and tools for effectively identifying and defining the priority targets for participatory variety development are provided in Weltzien, vom Brocke and Rattunde (2005) and in Chapter 4.

By explicitly defining the goals and expectations of a given population, parents can be selected that best contribute to the creation of the new population/variety with the desired genetic variability. Key questions for choosing parents include:

- What are the target environment(s), zone and group of farmers for whom the population should be of use?
- What is the acceptable range for critical adaptive and quality traits, such as maturity, grain type, biotic challenge resistances, and adaptation to specific soil and water regimes?
- What is the priority trait or combination of traits that are a target for improvement?
- What is the appropriate balance between level of diversity and eliteness?

The balance between level of diversity and eliteness is a critical issue in the choice and number of parents used for developing the population or variety. Maximizing the diversity of the population through selection of parents with outstanding performance for certain traits but less desirable for others will maximize the potential for long-term genetic gains, but reduce the possibility of deriving agronomically superior end products in the short term. In contrast, greater emphasis on population 'eliteness' through more restrictive inclusion of parents for population creation will maximize opportunities for immediate extraction of distinct finished varieties, but limit long-term potential gains and benefits from intra-varietal diversity.

12.6 MASS SELECTION

Mass selection involves the selection of individual plants or even of individual grains or seeds (Allard, 1999). This type of selection is based on the phenotype only, as a given genotype is neither replicated nor tested in differing environments. Mass selection therefore always has confounding of environmental conditions that can mask genotypic differences. As breeders can only marginally influence the extent to which observed differences are determined by genetic causes (h = square root of heritability), mass selection is only effective for traits with higher heritability and little genotype by environment interaction.

One factor that can be better managed to increase response to selection (R) is the intensity of selection (i) used in mass selection. As the test units are single plants it is relatively easy to increase selection intensity by increasing the area sown with the population bulk, to have a greater number of plants from which to select the minimum number of desirable plants to constitute the next cycle.

The extent of additive genetic variation that can be exploited by mass selection depends on the level of parental control. If the trait can be evaluated before flowering and undesirable plants culled, full parental control can be imposed and the full extent of additive genetic variance can be exploited. For traits that can only be observed after flowering, only the female parent can be controlled, and thus only 50 percent of σ_A can be exploited (Table 12.1), unless plants are self-pollinated and the selfed progenies are used for recombination.

12.6.1 For which selection objectives and conditions can mass selection be useful?

Mass selection is a very simple method of selection, as selection is based on individual plants. This method thus requires minimal materials and organization for implementation. Mass selection enables maintaining a very large effective population size even with high selection intensity. Several thousand plants can be evaluated and several hundred retained to create the next cycle of the population. An additional advantage of mass selection is that each season results in the recombination among differing gene blocks in the population. This frequent recombination is essential for breaking undesirable linkages and increasing the frequency of desirable trait combinations. This is very important during the initial phases of a recurrent selection programme, when new parental materials are being recombined to form new populations, or when a new variety is formed from partially inbred progenies.

Mass selection will be most effective for traits that are highly heritable, with genetic differences that are observable on individual plants. One study in pearl millet showed quite acceptable heritabilities for single plant expression of plant height (0.58), seed weight (0.52) and flowering date (0.45), but not for grain yield (0.29), based on parent-offspring regressions conducted in several populations (Rattunde, Witcombe and Singh, 1989). Thus mass selection for traits such as grain colour, grain size or form, plant height or time to flower can be effective, as these traits are expressed in a rather consistent manner, even with moderately heterogeneous soil conditions.

Mild selection with culling of undesirable types can be useful in newly created populations in which the introduction of new diversity or traits is accompanied by introduction of genes (or gene combinations) with undesired effects on quality or adaptation. This was the case in the early stages of the farmer-participatory population breeding work in Burkina Faso (Box 12.1). More intense selection can be applied when trying to concentrate favourable genes, for example with resistance to a pest or adaptation to specific conditions (as described in Box 12.2).

12.6.2 Potential roles and contributions of farmers

Mass selection is the method used by farmers for creating and maintaining the majority of the world's heritage of landrace varieties. Farmers are often skilled at single plant selection, with sophisticated mental indices for weighing several critical traits that are considered during selection, particularly for indigenous crops that they have developed over countless generations of selection. Sorghum farmers in Mali, for example, when choosing each panicle for use as seed consider several aspects of grain type (colour, size), glumes (ease of threshing) and panicle form (optimal density of grains and numbers of panicle branches, but with sufficient spacing to avoid risk of damage from insect feeding). Farmers may observe certain traits more accurately and with more practiced judgment than formal breeders, particularly for crops in their centres of origin or diversity. Likewise, farmers can weigh the importance of many traits, and set acceptable thresholds for each trait based on the importance of each to meeting their needs. Farmer mass selection also enables selection to be based on plant expression under their own field conditions. Involvement of farmers in mass selection also allows a larger scale of operation than would be possible for individual breeders, with possibilities of several farmers participating, each contributing their time and expertise to observe thousands of plants and select those showing most promise under their field conditions. Weltzien, vom Brocke and Rattunde (2005) propose options for farmer participation in mass selection.

12.6.3 Factors for success

The genetic gains achieved via mass selection can be maximized by attention to factors influencing the three components of the Selection Response Formula (see Chapter 2).

Heritability (h)

The appropriate choice of field and management of the field can help favour expression of genetic differences for the target trait(s). Pre-sowing observations of the terrain can help to chose sites where there is less soil heterogeneity, shading and nutrient effects of trees, piles of animal dung or residues from previous years. Likewise, the planning and uniform application of management practices should help favour expression of genetic differences for the desired target traits. Further, the standards for selection can be adjusted based on the apparent environmental conditions, relaxing standards in patches of poorer growth or raising standards in areas with exceptionally luxuriant growth. Gridded

BOX 12.1

Use of zone-specific sorghum populations as source material for variety development

Zone-specific broad-based sorghum populations were created to serve as sources of genetic diversity for deriving new varieties that combined increased grain productivity with the grain quality and adaptation of the farmer's own varieties for the Central-North (650 mm average annual rainfall), Central-West (800 mm) and Boucle de Mouhoun (900 mm) areas in Burkina Faso (vom Brocke *et al.*, 2008). As the parental materials were of diverse Guinea- and Caudatum-race origins, farmers applied mild selection for grain quality during the back-crossing and recombination cycles to increase the probability of deriving useful segregates for variety development in the resulting populations.

The varietal development process began in each of the three zones by two farmers, one per village, sowing approximately 10 000 plants of the zone-specific population in isolated fields representative of the most important production system in the area. A group of 10 to 25 farmers, both women and men, selected panicles from the population bulk, with each farmer choosing about three of the most desirable panicles for the specific grain or plant type of most interest to them. A total of about 250 panicles were selected per site, and thus 400 to 600 plants per population were selected with a selection intensity of about 2 to 3 percent. Selection by several farmers and in different field environments helped to better sample the plant types to address farmer's different needs and provide a sufficiently large number of progenies for appropriately intense selection in subsequent generations.

The S_1 lines obtained from the selected S_0 panicles were prepared in sets according to the 'variety type' category for which they were selected, and single-replicate nurseries were sown by individual farmers. Selection among and within progenies was applied according to normal pedigree variety development methods.

The fate of progenies selected out of the 2004 Boucle de Mouhoun population for variety development are tabulated below.

Variety type (primary selection criterion)	**2004**		**2005**			**2006**
	S_0 plants selected by farmers	**S_0 panicles (S_1 lines) retained by breeder**	**S_1 lines selected by farmers**	**Panicles ($S_{2.1}$ lines) selected by farmers in retained S_1 lines**	**S_2 lines retained by breeder**	**S_2 lines selected by farmers**
Couscous	8	6	3	3	3	2
Malting and beer	34	24	6	12	9	-
Food qualty (tô)	40	28	11	16	14	-
Commercial grain	31	24	8	11	7	-
Grain storability	27	19	6	7	3	-
Fodder	50	30	12	15	14	3
New panicle type	46	32	4	4	3	2
Early maturity	55	36	6	12	7	2
Striga resistance	31	22	10	17	12	-
Stems (construction)	39	26	10	10	4	1
Total	**361**	**247**	**76**	**107**	**76**	**10**

(K. vom Brocke, G. Trouches, C. Barro-Kondombo and J. Chantereau)

BOX 12.2

Origin of a flooding-tolerant sorghum population

ICRISAT-Mali conducted several cycles of mass selection in a broad-based random-mating sorghum population with genetic male sterility to recover the special Guinea-race glume and grain characteristics required for free threshing, resistance to grain mould and desirable food quality. The field where this population was grown in 2001 was flooded for three weeks when the river rose due to unusually heavy rains. The more desirable plants that survived that year were selected as probably possessing some tolerance to water logging, as the entire field was flooded. The same year, farmers expressed interest in having a sorghum variety for fields that tend to be inundated in years of heavy rainfall. The following year this ‘waterlogged’ cycle bulk was given to two farmers in different villages, who sowed it in low-lying fields adjacent to their own sorghum variety. The farmers liked the population very much, and one of them, Diakaridia Dembele, started selecting panicles within it for use as seed the following year. The next year the population performed exceptionally well and he selected panicles for seed for himself, but he also gave away 75 kg of seed in response to demand from many neighbours. Most of the farmers requesting seed were women who grow rice in low-lying areas and used this new sorghum ‘variety’ on the borders of their fields, where risk of temporary inundation was high. The farmer planned to continue selection in this population for one or two more seasons to obtain an acceptable level of uniformity for glume colour and panicle form, at which time he could consider it to be a finished variety.

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mass selection offers a systematic approach by dividing the field into grids, and selecting a common number of plants from within each grid.

The effectiveness of selection between plants can be maximized by ensuring that selection is conducted by the most skilled people. For example, the threshability (ease of separating grains and glumes) of sorghums in West Africa can be best observed by farmers who have years of experience and a cultural heritage of selection for this trait. Effectiveness of selection may be further raised by identifying individuals who are the most interested and locally respected for their capabilities as ‘seed experts’.

The genetic gains from mass selection in out-crossing species can be increased through parental control that reduces the extent to which selected plants are pollinated by unselected plants. Self pollination and selection of selfed plants achieves maximum parental control. The same result is achieved with populations of self-pollinating species containing genetic male sterility, through identification and selection of male-fertile plants. Note however that selection of selfed plants would require a separate recombination to constitute the next cycle bulk. If introgression from neighbouring fields is not desired, sufficient isolation distance would need to be maintained. Culling undesired plants prior to flowering also provides parental control and could therefore double gains for traits that can be observed before flowering. Culling out tall plants in a dwarf population is one such example.

Genetic Variance (σ_A)

The choice of parents for creating the initial population determines the level and usefulness of genetic diversity. The more diverse the parents chosen, the higher will be the expected genetic variance and therefore the potential gain from selection. There is usually an optimal level of diversity beyond which the mean performance of the population would go down, thereby reducing the usefulness of the population in the long-term (Schnell and Utz, 1975).

Maintaining sufficient population size through selection and recombination of a large enough number of plants will help maintain a desirable array of alleles, and assure genetic variation exists for selection in subsequent cycles (Witcombe and Virk, 2001). Likewise, maintaining a sufficiently large effective population size is indispensable to avoid inbreeding, which is of greatest concern in highly outcrossing species. It is exhibited as a loss of vigour of the population and undirected separation into distinctive lines due to random fixation of genes. Effects of inbreeding and strategies for avoidance are summarized by Allard (1999) and Hallauer and Miranda (1981), among others. Using a minimum of 200 plants to create the next cycle bulk will minimize loss of genetic variation and genetic drift that would otherwise arise from mating among a limited number of parents and sampling.

Mass selection, based on single plant selection in a given site, can produce more site-specific responses than would be obtained with multi-environment progeny testing. However, where the objective is to produce an improved population and eventual varieties with wider adaptation, a population may be grown by several farmers or researchers, with selections from differing sites being pooled by breeders to capture selections that represent a wider sample of conditions or selection criteria. Selections produced by different breeders on differing sites could be simply bulked, or they could be grown out in isolation for recombination, with eventual culling of certain off-type progenies.

Selection Intensity (i)

More intense selection (setting higher thresholds for retaining plants) is expected to increase the genetic gains. The selection intensity coefficient in the genetic gains formula corresponds to the number of standard deviations by which the mean of the selected fraction exceeds the population mean (Falconer, 1981; Becker, 1993), and thus depends on the percentage of selected individuals.

An advantage of mass selection is the possibility of achieving very high selection intensity, by which rare plants possessing the desired combination of several traits or express rare forms of a given trait can be identified. However, to realize this potential it is necessary that a sufficiently large number of plants be available for selection. For example, a population with 10 000 plants could be subjected to selection with a 2 percent selected fraction and still retain 200 plants for reconstituting the next cycle bulk. Observation of farmer selection in sorghum populations in Burkina Faso shows that they frequently retain selected fractions ranging from 0.2 to 5 percent.

12.7 PROGENY-BASED RECURRENT SELECTION METHODS

A range of methods for population improvement rely on testing, selecting and recombining families rather than individual

TABLE 12.2

Selection response per year for pearl millet head yield from alternative recurrent selection procedures using equal level of resources and optimized for allocation of labour

Recurrent selection procedure	Selection response
Mass selection(1)	0.22
Half-sib family(1)	0.34
Full-sib family	0.51
S_1 line (one stage)	0.27
S_2 line (one stage)	0.23
S_1 line (two stage)	0.26
S_1 line/S_2 line	0.26
Full-sib/S_1 line	0.46

Notes: (1) S_1 lines from S_0 single plants used for recombination.
SOURCE: as presented in Schipprack, 1993.

plants. These progeny-based methods may involve a single stage of selection or multi-stage methods that combine evaluation and selection of genetically different evaluation units and selection units in successive seasons or generations (Hallauer and Miranda, 1981; Schipprack, 1993). Superior progenies identified through this testing can be used in a pedigree breeding programme to directly develop new inbred varieties, or to develop parental lines for production of hybrids or synthetics (Box 12.4). For highly outcrossing species, superior progenies of similar agronomic type and maturities could be used to create new open-pollinated varieties by random mating.

The objectives pursued with progeny-based recurrent selection methods tend to be improvement of traits whose expression is unreliable on a single-plant basis, and the development of superior progenies or inbred lines. Increasing yield is a typical objective pursued by progeny-based selection methods, where replicated trials conducted in multiple environments are used to determine the genetic potential of the evaluation units. Modelling of expected selection responses of alternative recurrent-selection methods for pearl millet grain yield show that certain progeny-based selection schemes may achieve twice the genetic gain for grain yield compared with mass selection (Table 12.2), even with comparable allocation of resources and optimized for labour use (Schipprack, 1993).

Factors for success

Questions to consider for maximizing the response to selection include how many traits are to be improved and when selection for specific traits is conducted during the inbreeding process. Each additional selection criterion will reduce the potential gain for the individual characters. Farmer indications of acceptable thresholds and priorities for specific traits can be helpful to focus selection efforts. Selection for traits with higher heritabilities is recommended when single plant selections are used to generate progenies or in early generations. In contrast, selection for less heritable traits is best conducted in later generations when multiple-environment assessments are feasible and progenies are more homozygous.

Farmer's assistance in single plant selection can be useful to funnel the most promising genetic materials into further stages of testing, and thus use limited testing resources most effectively. Farmers can help create the progenies used to initiate the selection procedure through mass selection of half-sib or S_1 lines from recombined bulks. They can further assist by selection within progenies in on-station or on-farm nurseries. Selection by several farmers helps to retain diversity, especially as cultivar preferences may differ with differing socio-economic backgrounds or production objectives.

Effective population size is also important for progeny-based selection methods. Initial progeny trials should consist of at least 200 progenies that will allow an appropriate intensity of selection (15 to 30 percent) and still retain a sufficient number of progenies for recombination or a subsequent stage of selection. The initial creation of progenies (S_1, full-sib (FS) or half-sib (HS) for example) can thus be done by selection from thousands of plants. Mass selection by several farmers, each sowing the same bulk in their own fields, has been useful in achieving suitably large numbers of selected progenies.

Progeny evaluations conducted in sufficient test environments is also important to effectively assess genetic potential and to sample the environmental diversity. For example, the wide range of sowing dates, soil and rainfall conditions for sorghum production in even a single agro-ecological zone of West Africa requires a minimum of four to six test environments to provide some measure of representation. Conducting progeny trials on farmers' fields, although logistically challenging, can help achieve the necessary, and appropriate, sampling of test environments.

Progeny-based trials conducted with farmers presents several challenges not encountered with mass selection. The large number of progenies and more complicated trial designs requires researcher assistance, at least during planting and harvesting, or even researcher management of on-farm trials. Trial designs can be modified to make on-farm progeny testing feasible. Individual farmers could, for example, grow a single replication or even a subset (incomplete block) of test entries. Modern statistical procedures and computing power now make analysis of the widest range of incomplete and unbalanced designs possible. Issues of how benefits and costs are shared also need to be considered, since land and labour requirements may be much higher and direct benefits to participating farmers less than in the case of mass selection.

12.8 EVOLUTION OF POPULATION IMPROVEMENT PROGRAMMES

Although population improvement programmes can follow a single selection methodology for improvement of a given trait or set of traits over many cycles (Rattunde and Witcombe, 1993), this may not often be the case. Population improvement may begin by conducting several cycles of mass selection to narrow and 'clean up' the population to a more acceptable range for critical adaptation or quality traits. Populations may reach appropriate ranges for simply inherited traits after a few cycles of selection and little further progress will be made by selecting for these same traits. Improvement of more complexly-inherited traits, such as yield, would require changing to progeny-based selection methods.

Practical population improvement programmes can also undergo major changes in the breeding objectives in response to evolving needs and opportunities. For example, population improvement by ICRISAT-Mali was initially conducted on a sorghum population of tall plant height as this plant height corresponds to what most farmers grow in the target Sudanian zone of West Africa, and tall parental materials had the required suite of adaptive and quality characteristics. However, the convergence of farmers' priority setting that placed highest value on increased yields, the hypothesis that reducing heights could raise harvest index and thus grain yields, and the identification of novel dwarf segregants in the ongoing population improvement work, led to a major shift to dwarf population and variety development, as described in Box 12.3. Further, this sorghum population

BOX 12.3

The evolving Guinea-race sorghum populations in Mali

A broad-based sorghum population was developed as a source of diversity for breeding sorghum varieties with increased grain yield and the grain, glume and panicle characteristics required for adoption in the Sudanian zone of Senegal, Mali and Burkina Faso in West Africa. BC_1 or BC_2 progenies, created by crossing 13 higher yielding Guinea-landrace varieties to a source population segregating for the *ms3* genetic male-sterility gene locus, with subsequent backcrossing, were bulked together in 1994 (Rattunde *et al.*, 1997). Three cycles of recombination with mild selection and one cycle of more intense mass selection for grain and glume traits followed. Progeny-based selection was then initiated, using S_1 and S_2 progeny testing schemes, for increasing the population's yield level and to derive sorghum varieties with superior grain yield. This population and the varieties derived from it had plant heights of 3 to 5 m, similar to the landrace varieties used to create the population.

A new Dwarf Guinea Population was initiated in 1999 by selecting 50 plants with short stem-internodes (40 male-fertile and 10 male-sterile plants that gave $S_{0.1}$ and half-sib progenies, respectively) out of a total of 15 000 plants of the original tall Guinea Population These progenies were recombined together, as well as inter-mated with 12 dwarf progenies derived from previous population cycles and five short-statured inter-racial varieties produced by pedigree breeding. This new population was recombined, with the second cycle involving replicated randomized sowings of 240 F_1s to assure thorough recombination. The presence of desirable Guinea-race grain and panicle types on these markedly shorter plants (mean: 2.5 m) was confirmed by farmers, who identified approximately 200 superior S_0 plants.

Two hundred S_1 progenies, derived by selecting the most desirable S_0 male-fertile plants from the Dwarf Guinea Population, were tested in a replicated yield trial and selfed in a separate nursery to advance to the S_2 generation. A total 70 S_2 progenies from the highest yielding S_1 progenies were further evaluated for yield at the ICRISAT-Samanko station (two dates of sowing) and the IER-Kolombada (Mali) station the following year (2003). A total of 20 selected progenies were then recombined to create the cycle 2 bulk of the Dwarf Guinea Population. The recombination was conducted by first making paired crosses among progenies, and the following year random-mating in isolation of all crosses.

(F. Rattunde, E. Weltzien, A. Toure, J. Chantereau and C. Luce)

breeding programme will continue to adjust towards the emerging needs of dual-purpose (grain+fodder) varieties and of new short-statured lines as hybrid parents.

An even more rapid evolution of populations can occur in certain crops, like highly outcrossing pearl millet, where relatively few cycles of improvement are conducted between periodic crossing between populations (Rattunde *et al.*, 1997). This approach would require working with a number of different populations, and possible structured, diallel, population crossing to identify the most promising populations for continued improvement. By periodic inter-population crossing, heterosis could

BOX 12.4

Lata (Bala Berthe): A dwarf Guinea-race sorghum variety and hybrid parent developed through population breeding

S_3 progenies (n = 89) derived from the most promising S_2 progenies (see Box 12.3) were further tested in replicated, multi-environment, on-station trials for variety development. Six of the most promising progenies were included in a 16-entry, 2-replicate, early generation variety trial conducted by 20 farmers in 10 villages in 2005. Each entry was given a name to facilitate discussions by farmers. The progeny 'Lata' showed higher yield, intermediate height (2.5 m), and was appreciated by farmers. This progeny was given to Bala Berthe, a farmer with strong interest and expertise in selection. Bala Berthe conducted two cycles of mass selection for panicle architecture, grain and glume characteristics and shared a portion of his seed lot with ICRISAT. The variety Lata (Bala Berthe), following further testing in larger scale 4-entry 'Variety Test Kits', was submitted for variety registration in Mali. This variety was also used as a male parent to produce a series of experimental hybrids. Analysis of multi-environment hybrid yield trials showed that Lata (Bala Berthe) had the highest combining ability of all male parents in 2007.

be exploited, increasing the mean productivity as well as the genetic variation of the resulting inter-pool populations.

REFERENCES

Allard, R.W. 1999. *Principles of Plant Breeding*. New York, USA, John Wiley & Sons. 254 p.

Andrews, D.J., Gupta, S.C. & Singh, P. 1985. Registration of WC-C75 Pearl millet. *Crop Science*, 25: 199–200.

Becker, H. 1993. *Pflanzenzüchtung*. Stuttgart, Germany, Verlag Eugen Ulmer.

Falconer, D.S. 1981. *Introduction to quantitative genetics*. New York, USA, Longman. 340 p.

Fehr, W.R. (editor). 1987. *Principles of Cultivar Development*. Vol. 1 Theory and Technique. USA, MacGraw-Hill Inc.

Gallais, A. 1981. Amélioration des populations en vue de la création de variétés. *Le sélectionneur français*. pp. 5–23.

Hallaurer, A.R. & Miranda-Fo, J.B. 1981. *Quantitative Genetics in Maize Breeding*. Ames, USA, Iowa State University Press. 468 p.

Rai, K.N., Anand Kumar, K., Andrews, D.J., Rao, A.S., Raj, A.G.B. & Witcombe, J.R. 1990. Registration of ICTP 8203 Pearl Millet. *Crop Science*, 30: 959.

Rattunde, H.F., Witcombe, J.R. & Singh, P. 1989. Feasibility of mass selection in pearl millet. *Crop Science*, 29: 1423–1427.

Rattunde, H.F.W. & Witcombe, J.R. 1993. Recurrent selection for increased grain yield and resistance to downy mildew in pearl millet. *Plant Breeding*, 110: 63-72.

Rattunde, H.F.W., Weltzien-R., E., Bramel-Cox, P.J., Kofoid, K., Hash, C.T., Schipprack, W., Stenhouse, J.W. & Presterl, T. 1997. Population improvement of pearl millet and sorghum: current research, impact and issues for implementation. In *Genetic Improvement of Sorghum and Pearl Millet*, pp. 188–212. Proceedings of an International Conference held at Lubbock, USA, 23–27 September 1996.

Schnell, F.W. & Utz, H.F. 1975. F_1 Leistung und Elternwahl in der Züchtung von Selbstbefruchtern. *In* Bericht über die

Arbeitstagung der Vereinigung österreichischer Pflanzenzüchter, pp. 243–248. Gumpenstein, 25–27 November 1973. BAL, Gumpenstein, Austria.

Schipprack, W. 1993. Estimation of population parameters and optimization of alternative procedures of recurrent selection in Pearl Millet (*Pennisetum glaucum* (L.) R.Br.) PhD Dissertation. University of Hohenheim, Germany.

Singh, P., Raj, A.G.B., Rao, M.N.V.V. & Witcombe, J.R. 1994. Registration of 'ICMV 155' Pearl Millet. *Crop Science,* 34: 1409.

Strahwald, J.F. & Geiger, H.H. 1988. Theoretical studies on the usefulness of doubled haploids for improving the efficiency of RS in spring barley. *In* Proceedings of the 7th Meeting of Eucarpia Section on Biometrics in Plant Breeding. Ås, Norway, 2–5 August 1988.

vom Brocke, K., Trouches, G., Zongo, S., Bitie, A., Oualbéogo, A., Barro-Kondombo, C., Weltzien, E. & Chantereau, J. 2008. Création et amélioration in-situ de populations à base génétique large avec les agriculteurs au Burkina Faso. *Agriculture*, 17(2): 145–153.

Weltzien, E. 2005. Research on priority setting with farmers. *In* A. Christinck, E. Weltzien & V. Hoffmann, eds. *Setting breeding objectives and developing seed systems with farmers*. A handbook for practical use in participatory plant breeding projects. Weikersheim, Germany, Margraf Publishers.

Weltzien, E., vom Brocke, K. & Rattunde, F. 2005. Planning plant breeding activities with farmers. *In* A. Christinck, E. Weltzien & V. Hoffman, eds. *Setting breeding objectives and developing seed systems with farmers*. A handbook for practical use in participatory plant breeding projects. Weikersheim, Germany, Margraf Publishers.

Witcombe, J.R. & Virk, D.S. 2001 Number of crosses and population size for participatory and classical plant breeding. *Euphytica,* 122: 451–462.