

CHAPTER 13

Selection methods

Part 5: Breeding clonally propagated crops

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13.1 INTRODUCTION

The literature about participatory breeding of clonally propagated crops is very limited. This makes it difficult to write this chapter exclusively about how farmers have bred, how they breed—with or without support of scientists—and how they should breed clonally propagated crops. There are today clear definitions for participatory plant breeding (PPB), participatory variety selection (PVS) (see Chapter 9) and indigenous plant breeding (IPB; the selection process of farmers for more than 60 centuries). Breeding by scientists and economic entities has been redefined as formal plant breeding (FPB), consisting of breeding carried out on-station, linked with multi-location trials, and assisted by quantitative genetics, selection theory and biotechnology (with or without recombinant DNA technology). A variety developed through FPB is termed a modern variety (MV), in contrast to a farmer-bred variety (FV), which is developed by IPB. Especially in clonally propagated crops, FVs continue to dominate crop production in many developing world regions. Obviously FPB has not been so successful, because farmers decided to continue to grow FVs instead of adopting MVs (Friis-Hansen, 1992; Witcombe *et al.*, 1996). Definitions are helpful, providing a common term for the same technique or method. Here we need to bear in mind two points when considering such definitions and the issues associated with them:

- the every-day formula used to predict the response to selection (with all its extensions to several selection steps and traits) may well be the most useful tool given to breeding by statistics; and
- breeders have to adapt a crop to human needs and they must pay adequate attention to the needs of clients.

13.2 AN OVERVIEW OF CLONALLY PROPAGATED CROPS

What are clonally propagated crops?

Standard textbooks list a surprisingly large number of crops: all important root and tuber crops, many forage crops, nearly all types of fruit and wooden ornamentals, many cut flowers and pot plants, as well as forest trees. The definition of a clonally propagated crop is that the material to cultivate and maintain a variety is obtained by asexual reproduction, regardless of how different the plant material used for propagation is within and between species, encompassing tubers, roots, stem cuttings and corms, as well as asexually developed seeds (seeds developed without meiosis). It should be remembered that if crops such as maize (bred as an open-pollinated or hybrid crop) or beans (bred as a cross-fertilized, self-fertilized or hybrid crop) were to be propagated by stem cuttings or asexually developed seeds, they would be clonally propagated crops. In contrast, in breeding clonally propagated crops, the breeding techniques and methods that are usually associated with cross-fertilized and hybrid crops can be very useful. An example is the selection of parents in potato, cassava and sweet potato breeding, which are recombined in open-pollinated polycross nurseries to create new genetic variation. It is almost certain that techniques and methods from breeding cross-fertilized and hybrid crops will become much more important in the future of clone breeding.

What is the general principle in breeding clonally propagated crops?

It appears to be simple: to break the normal clonal propagation by a crossing step, and thus develop sexual seeds and genetic variation from which to select new clones. All propagation steps from the first to the last

selection step are again 'normal' asexual reproduction (Simmonds, 1979). Hence, the finally selected clone is genetically identical with the original seed plant from which the selected clone is derived. In other words, each seed plant is a potential variety. Roots and tubers, fruit and tree plant species have been used by human since long before the dawn of agriculture. They have been domesticated by IPB (Simmonds, 1979) and several made a substantial yield progress by FPB in some regions of the world. However, in other regions of the world there is not much yield progress, and in these regions there appears to be a clear need of PPB for progress. We wish to illustrate this by two examples: potato and sweet potato.

An example of the needs and requirements of clonally propagated varieties can be found in potato (*Solanum* spp.). There are about 200 wild potato species (Huamán and Ross, 1985). They usually contain glycoalkaloids, which give tubers a bitter taste and which are toxic when consumed in large quantities (Zitnak and Filadelfi, 1985). It is nearly certain that 100 to 130 centuries ago indigenous knowledge in the Andes and along the Pacific coast of South America was those sites where it was possible to collect wild potato tubers where species and mutants were growing that had low alkaloid content. Although these tubers were very small, the man, or more probably a woman, made life much easier by growing and maintaining desirable types by cloning close to their homes. This happened more than 8 000 years ago, and most likely independently at several places (Ugent, Pozorski and Pozorski, 1982; Ugent, Dillehay and Ramirez, 1987). Those types were preferred that were easier to maintain, easier to harvest (shorter stolons) and had larger tubers compared to other types. The

result was the domestication of *pitiqiña* (*Solanum stenotomum*), which was most probably selected from *S. leptophyes* or *S. canasense*. From the view-point of the knowledge of the twenty-first century it is not surprising that suddenly potato plants with larger leaves and larger tubers were found. Potato spontaneously changes its polyploidy level by unreduced gametes and recombination. Polyploid potatoes are more vigorous than their diploid ancestors. The result was the domesticated of polyploid *andigena* (*S. tuberosum* subsp. *andigena*). *Andigena* is the ancestor of the commercial potato in long-day temperate climates—the so-called *Irish potato* (*S. tuberosum* subsp. *tuberosum*) (Hawkes, 1979, 1981). This IPB of potato and introductions of FV of potato into the Northern Hemisphere changed the world both socio-economically and politically (Hobhouse, 1985).

Today, eight species of potato are still cultivated in the Andes, variously diploid, triploid, tetraploid and pentaploid:

- (i) cultivated diploid potatoes are *pitiqiña* (*S. stenotomum*), its close relatives *phureja* (*S. phureja*) and *limeña* (*S. goniocalyx*), and *ajanhuiri* (*S. ajanhuiri*), which evolved from interspecific recombination of diploid *pitiqiña* and the diploid wild potato species *S. megistacrolobum*;
- (ii) cultivated triploid potatoes are *chaucha* (*Solanum* × *chaucha*), a hybrid between diploid *pitiqiña* and tetraploid *andigena*, and *rucki* (*Solanum* × *juzepczukii*), a hybrid between diploid *pitiqiña* and the tetraploid wild potato species *S. acaule*;
- (iii) cultivated tetraploid potatoes are *andigena* and *Irish potato*; and finally
- (iv) the cultivated pentaploid potato is a hybrid species (*Solanum* ×

curtilobum), which evolved between tetraploid andigena and triploid rucki, and unfortunately is also called rucki (Hawkes, 1981; NRC, 1989).

The andigena is the best known potato in the Andes (with about 2 500 known FVs). It is cultivated in tropical mid-elevation valleys and mountainsides. The second most important potato is phureja, which is cultivated on the warm and moist eastern slopes of the Andes (with about 500 known FVs), followed by *limeña*, ajanhuri and rucki. Limeña or *papa amarilla* is grown in the temperate areas of the Andes and still achieves high market prices due to its taste and flavour. Ajanhuri and rucki are the most frost resistant cultivated potato species and cultivated up 4 200 masl. The former is used as an insurance crop in cases where andigena fails due to unpredictable hail and frost (some ajanhuri varieties are bitter and must be processed). The latter are usually only eaten after having been processed into *chuño*, the famous storable food product of the Incas. Many of these potatoes have clearly better taste and flavour compared with what is considered potato in the Northern Hemisphere (Huamán 1983; NRC, 1989; De Haan, 2009). However, taste is a variable characteristic; it changes from person to person, from family to family, and from society to society. Moreover, many of these IPB potatoes are clearly superior in protein and micronutrient concentration in their tubers (pro-vitamin A, calcium, magnesium, iron and zinc) compared with MVs (Ochoa, 1990; Morris *et al.*, 2004; Burgos *et al.*, 2008), and are useful as genetic resources or directly as FVs to alleviate malnutrition in the mountain regions of the world.

The potato and the Andes were chosen as an example to give an impression of an aspect of breeding that is as least as

important as taste, flavour and nutrient content, namely the importance of adaptation of a crop and its varieties to the local environment. They who know the Andes also know that is unrealistic to breed a widely adapted potato variety for this region of the world. Temperature, rainfall, soil conditions (including salinity and drought) and pest and disease pressures change from microclimate to microclimate from sea level at the Pacific coast up to 3 500 to 4 500 masl in the Andean highlands (mid-elevation valleys and plateaus), and again down into the warm tropics, where the Andes meet the Amazon. Breeding potatoes in this region of the world was and can only be successful by decentralization and with farmer participation (Johns and Keen, 1986; Gabriel and Torrez, 2000). Admittedly this is an extreme example, but such situations can be found in less extreme form in nearly all regions of the world. In the Southern and Northern Hemispheres, potatoes generally must be day-neutral; in South-west and Central Asia, potatoes must be very quick to mature, with a short crop duration of 80 to 90 days; in Europe and Northern America, more than 30 quality characteristics combine to determine tuber quality for market needs; and finally in the UK, a potato variety must be white fleshed, whereas in Germany it must be yellow fleshed, otherwise it is not eaten (CIP, 1984; Levy, 1984; Tarn *et al.*, 1992). An additional major factor for adaptation and acceptance of potato varieties is their tolerance and resistance to diseases and pest. In all temperate and moist climates, potato farmers have to fear Late blight (*Phytophthora infestans*), which is not important at temperature above 25°C, but then Early blight (*Alternaria solani*) takes over. In tropical lowlands, the farmer has to fear Bacterial wilt (*Pseudomonas solanacearum*), and in all warm dry regions

the potato crop can be lost because of Colorado beetle (*Leptinotaras decemlineata*) (CIP, 1977, 1980; Radcliffe, 1982; Rich, 1983).

A simpler example for the needs and requirements of clonally propagated varieties can be found in sweet potato (*Ipomoea batatas*). Sweet potato was domesticated in the Americas more or less during the same prehistoric period as the potato (O'Brien, 1972). The evolution of sweet potato was not as complex and diverse as that of potato. There are about 500 *Ipomoea* species, but only the *I. batatas* species was domesticated (Austin and Huamán, 1996). Again polyploidy was important. Sweet potato is hexaploid and its closest relative is *I. trifida* (di- and tetraploid). It is certain that sweet potato contains the *I. trifida* genome, but obviously it is not simply a multiple copy. Two-thirds of the sweet potato genome corresponds to the *I. trifida* genome and one-third to an ancestor very closely related to *I. trifida* (Shiotani and Kawase, 1989). Within diploid *I. trifida* accessions (seed families) it is also possible to find plants that form small storage roots (Daniel Reynoso, pers. comm.). However, sweet potato has been found in the ruins of the so-far oldest city in the Americas, *Caral* on the Pacific coast of central Peru (Solis, 2004), and the crop reached Pacific Polynesia and parts of South-East Asia (naturally or by early seafarers) before Columbus. It was primarily the Portuguese that introduced it into Europe, Africa, South Asia and East and South-East Asia (Yen, 1976).

Although the taste of sweet potato in FVs and MVs differ tremendously, two major types can be distinguished: (i) the orange-fleshed, moist, low dry matter (DM) and sweet type, which has a soft mouth feeling; and (ii) the white- or pale-yellow-fleshed,

high DM, low-sweet or bland type, which has a dry mouth feeling. The first type, also called the dessert type, has extremely high pro-vitamin A concentrations (Huang, Tanudjaja and Lum, 1999) and a 50 g piece of fresh storage roots can meet the daily requirements of a pre-schooler (Low *et al.*, 2007). Moreover, sweet potatoes with high pro-vitamin A concentrations have high protein and mineral concentrations (Grüneberg, unpublished). In the United States of America, the dessert type is generally the desired sweet potato to meet market and consumer needs. In the Caribbean, low DM orange-fleshed sweet potatoes (OFSP) are consumed, but as a staple, so a dryer mouth feel and less sweet flavour is preferred. These white- or yellow-fleshed varieties are known as *bonitos* or *ricos* (Baynes, 1972). Along the Pacific coast of South America we observed that sweet potatoes are mainly pale orange fleshed and less sweet. However, locally, white- and purple-fleshed sweet potatoes are consumed, which clearly have different taste, texture and flavour compared to OFSP. In Brazil, the sweet potato storage roots must clearly have a high DM concentration (28 to 30 percent DM), and usually this is a white-fleshed sweet potato; however, locally, high DM OFSP can be found (Amauri Buso, pers. comm.).

The taste preferences in sub-Saharan Africa are similar to those in Brazil, perhaps because the Portuguese introduced the sweet potato into Africa. All FVs are nearly exclusively white- or yellow-fleshed and have high DM concentrations; however, a few pale- to medium-orange-fleshed FVs can be found with high DM concentrations (Tumwegamire, unpublished). These local OFSP FVs are very promising for alleviation of vitamin A deficiency in sub-Saharan Africa (e.g. FVs such as 'Ejumula', 'Carrot

C', 'Carrot Dar es Salaam' or 'Zambezi'). In eastern Africa, storage root DM contents must be >30 percent (Mwanga *et al.*, 2003). In southern Africa, storage DM concentration between 26 and 29 percent are accepted (Laurie Sunette, pers. comm.), whereas in West Africa, sweet potato must be non-sweet, very high in DM concentrations (between 30 and 35 percent DM) and with a texture and flavour tentatively similar to yam (*Dioscorea* spp.) (IITA, 1981). In contrast, in India, where sweet potato consumption has been very low in the past, today people prefer sweet potatoes with high DM, high sugar content, dark orange flesh and a storage root shape that is cylindrical but tapering at both ends (Sreekanth Attaluri, pers. comm.).

In addition to regional and local preferences for storage-root colour, DM, texture and taste, the acceptability of sweet potato varieties is mainly determined by pest and disease pressures. However, the number of pest and diseases in sweet potato are considerable lower than in potato. Generally, sweet potato varieties must have a certain degree of tolerance to Sweet potato virus disease (SPVD). The disease occurs after infection by two viruses: the Sweet potato feathery mottle virus (SPFMV) and the Sweet potato chlorotic stunt virus (SPCSV). The SPCSV is the more problematic component of SPVD, because yield losses due to SPFMV, in the absence of SPCSV co-infection, are low and SPFMV resistance in sweet potato breaks after the plant is infected by SPCSV (Gibson *et al.*, 1998; Karyeija *et al.*, 2000). SPVD often causes serious yield losses in high-virus-pressure zones of sub-Saharan Africa, and American OFSPs have failed in many regions of sub-Saharan Africa due to insufficient SPVD tolerance. Although the virus pressure of SPVD along the Pacific coast of South America is not extreme,

farmers have not adopted MVs (e.g. cv. INA100, which is a high yielding OFSP and fits consumer needs very well), because of insufficient SPVD tolerance. Farmers became disappointed with new MVs and after a few growing seasons returned to FVs such as cv. Jonathan and cv. Huambachero. OFSPs from the Americas with elevated DM (e.g. cv. Jonathan) are partially successful in southern Africa, and in south-west and central Asia, provided that weevil pressure is not extreme. Weevil damage is associated with drought-prone regions (Central and South America, sub-Saharan Africa and south-west and central Asia); however, weevil species differ: *Cylas formicarius* in all parts of the tropics, *C. puncticollis* additionally in Africa, and *Euscepes postfasciatus* in the West Indies. On-station and farmers' field experiments show that there are significant differences in weevil tolerance among sweet potato genotypes (Hahn and Leuschner, 1981), but this tolerance appears to be less pronounced or inexistent on-farm. At the same time, farmers in drought-prone regions of Malawi want sweet potatoes in which storage roots are formed deep in the soil and which are clearly tapering at the top, because they associate this with less weevil damage (Ibrahim Benesi, pers. comm.). Moreover, latex in the storage root skin has been associated with less weevil damage by farmers, and varieties like Santo Amaro from Brazil clearly have considerably less weevil damage than other sweet potato varieties (Rafael Vasquez Martinez, pers. comm.).

The International Potato Center (CIP) is promoting OFSPs to alleviate vitamin A deficiency in the world (Low *et al.*, 2007; Pfeiffer and McClafferty, 2007). However, introductions from the Americas failed in the high-SPVD-pressure zone of eastern Africa (as did the FV Jonathan). To a certain extent this was associated with the

storage root flesh colour and taste. At the same time, local African OFSP FVs, such as Ejumula, Carrot C, Carrot Dar es Salaam and Zambezi, and locally-bred OFSP MVs, such as NASPOT5 (Mwanga *et al.*, 2003), have been adopted after awareness campaigns on the vitamin A deficiency problem (Regina Kapinga, pers. comm.). For this reason, CIP puts emphasis on decentralized sweet potato breeding, and has recently started to recommend incorporation of at least one participatory selection step in the breeding process.

In sweet potato breeding for human consumption, decentralization is characterized by a general overall goal: that of developing more OFSP varieties that meet local needs and consumer preferences, to alleviate hunger and malnutrition and to improve public health. The emphasis is on organizing OFSP breeding in eastern and southern Africa, with national OFSP breeding programmes starting recently in West Africa (Ghana and Nigeria) and south-west and central Asia (India, Bangladesh and Sri Lanka). Breeding is almost exclusively carried out by national agricultural research system (NARS) breeders and on NARS breeding stations, with currently 12 NARS and two sweet potato breeders from the CGIAR system involved. NARS breeders are provided with funds for parental recombination and to consider the quality trait of storage root flesh colour in the breeding process. Main emphasis in breeding is given to: (1) material exchange at the seed and clone level, (2) exchange of information, knowledge and results from breeding trials by annual meetings, reports and back-stop visits, and (3) a sweet potato breeding research and training build up on the needs shaped among discussions between NARS and CGIAR breeders. This has resulted in an additional aim to build

up regional platforms for sweet potato breeding in eastern, southern and West Africa, with a focus on dual purpose OFSP (human consumption and animal feed), drought tolerant OFSP, and non-sweet high DM OFSP. PPB has so far mainly been a research component in the organization of sweet potato breeding.

There are strong indications that PPB in early selection steps of the sweet potato breeding process increases the efficiency and minimizes the risk of making wrong selection decisions. In contrast to PPB, PVS is tentatively a form of on-farm evaluation (in the frame of a larger number of multi-location trials) and cannot be as efficient as PPB, because there is considerably less genetic variation, and, for highly heritable traits, there is nearly no genetic variation at later breeding stages among clones. Not surprisingly, akin to the role of IPB in potato crop evolution, it has been shown that farmers have the ability to manage selection stages in sweet potato (Gibson *et al.*, 2008). This is consistent with results for potato (Gabriel and Torrez, 2000) and cassava (Manu-Aduening *et al.*, 2006). Farmer selections are mainly made by visual screening. This includes quality characteristics, diseases and pests, as well as the growth type, which is to a certain extent associated with drought adaptation in sweet potato (see below on selection in early breeding stages). Most importantly, farmers use more criteria and characters to select sweet potato clones than do breeders in FPB (Gibson *et al.*, 2008). In such a situation, the risk of FPB is to ignore characters that are important for good overall performance of a clonal variety. However, in the study of Gibson *et al.* (2008) in three provinces in Uganda, the most important characteristics for selection by farmers in early selection stages were common to those used by

breeders, as were their relative weighting of characters, namely: (i) good root yield and big roots > (ii) SPVD tolerance or resistance > (iii) tolerance to drought, attractive root colour prior to cooking, straight root shape and orange- or yellow-flesh storage-root colour, and finally > (iv) tolerance to weevils. Characters of storage roots after cooking were not determined. It should be noted that in later selection stages (FVS) the priority list of farmers or relative character weights changed, namely: (i) good root yield, big roots, drought tolerance, sweet and mealy roots after cooking > (ii) early root maturity, continuous root yield for piecemeal harvesting, and weevil tolerance > (iii) long root storage in the soil, extensive foliage, tolerance to caterpillars (*Acraea acerata*), marketability, attractive colour of storage roots prior to cooking, and non-fibrous roots after cooking > (iv) followed by a group of characteristics with very low weights, such as good root yield in poor soils, good vine establishment, tolerance to rats and other vertebrates, non-sappy and no loss of taste in storage roots prior to cooking, soft texture, nice looking at the table, nice flavour and easy or quick to cook storage roots. For some characters (mainly biotic pressures, i.e. SPVD and weevil tolerance; Gibson *et al.*, 2008) there were clearly different weights given to characters in different provinces, which might reflect local biotic challenge. Moreover, farmers used more attributes (51 attributes) than scientists and breeders (11 attributes) to describe and distinguish varieties. To what extent this is important is not clear; however, it might show the importance to farmers of distinguishing varieties.

To summarize:

- (i) not surprisingly, farmers have the ability to select successfully both in the early and later breeding stages of

a breeding programme (Gabriel and Torrez, 2000; Manu-Aduening *et al.*, 2006; Gibson *et al.*, 2008);

- (ii) selection by farmers, mainly by visual screening, is more efficient in earlier stages than in later stages of the breeding programme, which can also be explained by the larger genetic variation in early selection stages compared with later stages in breeding clonally propagated crops; and
- (iii) so far, selection by farmers at early selection stages has only been applied to a sample of the genetic variation generated by FPB in crossing programmes and it must be more efficient to expose the full genetic variation to farmer selection in the breeding process.

In Sections 13.2 and 13.3 we suggest how this can be done in a cost-efficient way and without losing time in the breeding process. However, doubts remain as to whether farmers can efficiently use and treat large amounts of true seeds and true seed plants, which often appear in quite different amounts per cross combination and have quite different performance compared with plants grown from vegetative plant parts. It might be more useful that plant breeders germinate seeds and multiply for each family a reasonable numbers of clones so that farmers can select clones in small plots comprising a few plants (2 to 4 per genotype). A further advantage of this is that the breeder can use the frequency of selected clones per family by the farmer as additional information to identify appropriate parents for recombination. However, we think that the selection of parents in breeding clonally propagated crops should have a participatory component, but should be mainly carried out by the breeder due to the genetics (see Section 13.2) and statistics

(see Section 13.5) involved in appropriate choices of parents in breeding clonally propagated crops.

To consider the range of needs, preferences and adaptation requirements for the large number of clonally propagated crops is out of scope in this chapter. Here we want to give the principles of breeding clonally propagated crops and how PPB can be carried out or linked into these breeding programmes. The breeding objectives and methods will be considered for four agricultural crops in more detail at the end of this chapter, namely: potato, sweet potato, cassava, and banana or plantain. Table 13.1 gives the plant parts used for propagation, the world production and the area harvested, as well as the polyploid level of the most important clonally propagated crops in agriculture. Obviously, quality characteristics determined by consumer preferences and market needs are key characteristics for breeding clonally propagated crops, because many of these

are eaten fresh, or are only boiled or roasted, and when they are processed this is often carried out at the household level. Exceptions are sugar cane, fruit crops used for the juice industry, and to certain extent root and tuber crops (potato, cassava and sweet potato) when they are used for the starch, alcohol or biofuel industries. In resource-poor environments, yields and yield stability with low input are a priority, in addition to consumer acceptability. As has been mentioned above, a major factor that determines yields, yield stability and adaptation are pests and diseases. The most important pests and diseases of important clonally propagated crops in agriculture by eco-geographical region are given in Table 13.2, together with the most important quality characteristics.

Most clonally propagated crops are polyploid (Table 13.1). An exception is cassava, which can be considered as a polyploid behaving like a diploid (see below). Polyploidy is an important aspect

TABLE 13.1
Data on the 11 most important clonally propagated crops on a global basis

Species	Planting material	World production [†]	Area harvested [†]	Polyploidy
Potato (<i>Solanum tuberosum</i>)	Sprout tubers	315 × 10 ⁶ t	18.8 × 10 ⁶ ha	2x, 3x, 4x, 5x
Cassava (<i>Manihot esculenta</i>)	Hardwood cuttings	226 × 10 ⁶ t	18.6 × 10 ⁶ ha	2x
Sweet potato (<i>Ipomoea batatas</i>)	Sprout cuttings	124 × 10 ⁶ t	9 × 10 ⁶ ha	6x
Yam (<i>Dioscorea</i> spp.)	Root tubers	51 × 10 ⁶ t	4.6 × 10 ⁶ ha	3x–10x
Taro (<i>Colocasia esculenta</i>)	Corms	12 × 10 ⁶ t	1.8 × 10 ⁶ ha	4x
Sugar cane (<i>Saccharum officinarum</i>)	Cane stalks	194 × 10 ⁶ t ‡	20.4 × 10 ⁶ ha	8x
Banana and Plantain (<i>Musa × paradisiaca</i>)	Corms	105 × 10 ⁶ t	9.6 × 10 ⁶ ha	3x
Citrus fruit (<i>Citrus</i> spp.)	Bud stick grafting on rootstocks	89 × 10 ⁶ t	5.6 × 10 ⁶ ha	2x, 3x+1, 4x-3
Grapes (<i>Vitis vinifera</i>)	Hardwood cuttings	69 × 10 ⁶ t	7.4 × 10 ⁶ ha	6x
Apple (<i>Malus pumila</i>)	Bud stick grafting on rootstocks	64 × 10 ⁶ t	4.8 × 10 ⁶ ha	2x, 3x
Strawberry (<i>Fragaria grandiflora</i>)	Adventitious shoots	4 × 10 ⁶ t	0.26 × 10 ⁶ ha	8x

NOTES: † FAOStat 2006 at faostat.fao.org, ‡ Sucrose production.

TABLE 13.2

Quality characteristics, pests and diseases by production zone of the 11 most important clonally propagated crops in agriculture and horticulture

Major production zones	Quality characteristics	Pest and diseases
Potato (<i>Solanum tuberosum</i>)		
Tropical highlands	Various fresh consumption traits, high iron and zinc contents, adaptation to various micro-climates	Late blight (<i>Phytophthora infestans</i>), cutworms (<i>Agrotis</i> spp.), potato tuber moth (<i>Phthorimaea</i> spp.)
Tropical lowlands	More uniform fresh consumption traits, high iron and zinc contents, extremely short crop duration (<80 days)	Bacterial wilt (<i>Pseudomonas</i> spp.), Early blight (<i>Alternaria solani</i>), Root-knot nematode (<i>Meloidogyne</i> spp.), viruses (Potato leaf roll virus (PLRV), Potato virus Y (PVY), etc.), year round aphid pressure
Temperate zones	Various fresh consumption traits, high starch for industrial use, various processing traits (chips, French fries)	Late blight, cyst-forming nematodes, (<i>Globodera</i> spp.), potato virus diseases (PLRV, PVY, PVX, etc.)
Cassava (<i>Manihot esculenta</i>)		
Humid tropics	Cooking quality, elevated provitamin A content for human consumption with low HCN content, high DM for industrial uses	Bacterial blight (<i>Xanthomonas axonopodis</i>) in Asia, Africa and the Americas, Frogskin disease (CFSD) in the Americas
Drought-prone tropics	Cooking and processing (fried cassava, gari, fufu) quality, elevated provitamin A content for human consumption with low HCN content, high DM for industrial uses	African cassava mosaic (CMD) virus and Cassava brown streak disease (CBSD) in Africa, Green mite (<i>Mononychellus tanajoa</i>) and mealybugs (<i>Phenacoccus</i> spp.) in Africa and the Americas
Sweet potato (<i>Ipomoea batatas</i>)		
Humid tropics	High DM WFSP and OFSP	Extreme Sweet potato virus disease (SPVD), especially in eastern Africa
Drought-prone tropics	Elevated DM WFSP and OFSP, and clearly non-sweet in West Africa	Sweet potato weevils (<i>Cylas</i> spp.) and SPVD to a lesser extent
Tropical highlands	Elevated DM	<i>Alternaria</i> spp. and SPVD to a lesser extent
Temperate zones	OFSP with low DM and WFSP with high DM (both with medium sugar content)	Root-knot nematode (<i>Meloidogyne</i> spp.) and SPVD to a lesser extent
Yam (<i>Dioscorea</i> spp.)		
Humid tropics	Thirteen species with regional importance (main species <i>D. rotundata</i>), majority in wet hot tropics, but <i>D. abyssinica</i> , <i>D. alata</i> and <i>D. esculenta</i> also in dryer regions due to dormancy of tubers; growing time and taste varies extremely among species (some are poisonous and must be cooked)	Yam tuber beetles (<i>Heteroligus</i> spp.) and Anthracnose (<i>Colletotrichum</i> spp.), especially in West Africa, Yam nematode (<i>Scutellonema bradys</i>), Root-knot nematode (<i>Meloidogyne</i> spp.) and Shoe string virus disease
Taro (<i>Colocasia esculenta</i>)		
Humid tropics	<i>Colocasia</i> cultivar groups: (1) one large corm with few cormels; and (2) several small cormels. Genotypes have very different shelf lives (dormancy period) and some require excessive processing before edible	Corm and root rots (caused by <i>Pythium</i> spp., <i>Phytophthora</i> spp., <i>Rhizoctonia</i> spp. and <i>Erwinia</i> spp.) and Dasheen mosaic virus (DMV) across world regions, Taro blight (<i>Phytophthora colocasiae</i>) and Taro beetle (<i>Papuana</i> spp.), especially in the South Pacific
Sugar cane (<i>Saccharum officinarum</i>)		
All regions	Weight of canes, sugar content, juice purity, short or long vegetative times and adaptation to photoperiod (non-flowering)	In the past, virus diseases were most important; today they play a subordinate role due to resistance breeding and virus-free planting materials Pineapple disease (<i>Ceratocystis paradoxa</i>), Red rot (<i>Colletotrichum falcatum</i>), Smut (<i>Ustilago citaminea</i>), Shoot and Internode Borer (<i>Chilo</i> spp.) in nearly all regions
Humid tropics		Yellow leaf spot (<i>Cercospora</i> spp.), Scale insect (<i>Melanaspis glomerata</i>), Pyrrilla (<i>Pyrrilla purpusilla</i>)
Drought-prone tropics and subtropics		Eye spot (<i>Drechslera sacchari</i>), Whitefly (<i>Aleurolobus barodensis</i>)
Tropical highlands		Leaf scald (<i>Xanthomonas albilineans</i>), Wilt (<i>Cephalosporium sacchari</i>)

Major production zones	Quality characteristics	Pest and diseases
Banana and plantain (<i>Musa x paradisiaca</i>)		
Humid tropics and subtropics	Bananas have a lower DM and higher sugar contents (very narrow genetic variation in triploid gene pool – ca. 30 cvs.) compared with high DM and starchy plantains (larger genetic variation in triploid gene pool – ca. 125 cvs.). Plantains are important staples in Central Africa and some parts of South America.	Banana wilt (<i>Fusarium oxysporum</i>) especially in the Americas, Yellow sigatoka (<i>Mycosphaerella musicola</i>), Black sigatoka (<i>M. fijiensis</i>) especially in Asia, Moko disease (<i>Pseudomonas solanacearum</i>), Bunchy top virus, nematodes such as <i>Radopholus similis</i> , banana root borer (<i>Cosmopolites sordidus</i>)
Citrus fruit (<i>Citrus</i> spp.). Cultivated citrus may be derived from as few as four species: Key Lime (<i>C. aurantifolia</i>), Pomelo (<i>C. maxima</i>), Citron (<i>C. medica</i>) and Mandarin (<i>C. reticulata</i>). All other “species” are hybrids		
All regions	Very different tastes and fruit sizes (oranges — ca. 1100 cvs.; mandarins, lemons, pomelo). Citrus trees hybridize very readily and new hybrids easily maintained by apomixis.	Strong rootstock influence (<i>C. jambhiri</i> , <i>C. resnyi</i> , <i>Poncirus trifoliata</i>) in adaptation to cold and resistance to <i>Phytophthora</i> root rot and virus diseases such as Tristeza, Porosis and Exocortis
Subtropics		Citrus canker (<i>Xanthomonas citri</i>), Foot rot (<i>Phytophthora</i> spp.), Melanose (<i>Diaporthe citri</i>), Blue and green mould (<i>Penicillium</i> spp.), Tristeza virus, nematodes such as <i>Tylenchulus semipenetrans</i> , fruit fly (<i>Bactrocera</i> spp.)
Drought-prone tropics		Foot rot (<i>Phytophthora</i> spp.), Gummosis (<i>Phytophthora</i> spp.), Citrus scab (<i>Elsinoe fawcetti</i>), Tristeza virus, Porosis viruses, fruit fly (<i>Bactrocera</i> spp.), citrus psyllid (<i>Diaphorina citri</i>), moth species such as <i>Ophideres</i> , <i>Sphingomorpha</i> , etc.
Grapes (<i>Vitis vinifera</i>) North American species: <i>V. aestivalis</i>, <i>V. labrusca</i>, <i>V. rotundifolia</i>		
Temperate zones	The North American species are of interest for the summer rainfall regions in the tropics because of their disease resistance and minimal chilling requirement – especially in crosses with <i>V. vinifera</i> (better taste, better texture of berries)	Bunch rot (<i>Botrytis cinerea</i>), Downy mildew (<i>Peronospora sparsa</i>), Powdery mildew (<i>Erysiphe necator</i>), vine moths (<i>Eupoecilia ambiguella</i> , <i>Lobesia botrana</i>), eriophyid mite (<i>Calepitrimerus vitis</i>)
Drought-prone tropics and subtropics		Downy mildew, powdery mildew, Anthracnose (<i>Elsinoe ampelia</i>), beetles such as <i>Popillia japonica</i> , thrips (<i>Scirtothrips dorsalis</i> , <i>Thrips hawaiiensis</i> and <i>Rhipiphorothrips cruentatus</i>), grape root borer (<i>Vitacea polistiformis</i>), bugs such as <i>Lygocoris inconspicuous</i> , Grape mealybug (<i>Pseudococcus maritimus</i>)
Apple (<i>Malus pumila</i>)		
Temperate zones	There are large differences in vernalization need among cultivars and several can be grown very successful in Mediterranean climates. Some cultivars in higher places in the equatorial region if the leaves are removed before beginning of bud dormancy (stripping off, or chemical defoliation)	Fireblight (<i>Erwina amylovora</i>), Apple rust (<i>Gymnosporangium</i> spp.), Apple scab (<i>Venturia inaequalis</i>), Plum curculio (<i>Conotrachelus nenuphar</i>), Apple maggot (<i>Rhagoletis pomonella</i>), Codling moth (<i>Cydia pomonella</i>)
Subtropics		Apple scab, Powdery mildew (<i>Podosphaera leucotricha</i>), Crown rot (<i>Phytophthora cactorum</i>), Apple crown gall (<i>Agrobacterium tumefaciens</i>), Bitter rot (<i>Glomerella cingulata</i>), root rots (<i>Phytophthora</i> spp.), Woolly apple aphid (<i>Eriosoma lanigerum</i>), Apple sawfly (<i>Hoplocampa testudinea</i>), Green apple aphid (<i>Aphis pomi</i>)
Tropical Highlands		Fireblight, Crown rot, Woolly apple aphid
Strawberry (<i>Fragaria xananassa</i>)		
Subtropics and temperate zones	Ancient cross of <i>F. virginiana</i> (8x) from eastern North America and <i>F. chiloensis</i> (8x) from Chile	Grey mould (<i>Botrytis cinerea</i>), Powdery mildew (<i>Sphaerotheca macularis</i>), Strawberry blossom weevil (<i>Anthonomus rubi</i>), European tarnished plant bug (<i>Lygus rugulipennis</i>)

in crop evolution (as we have already seen in potato) and has important consequences in breeding clonally propagated crops. It is important to note that all ‘breeding lines’ or varieties of clonally propagated crops are homogenous (clone lines and varieties are genetically fixed and as homogenous as non-segregating breeding lines or hybrids from breeding self-fertilized or hybrid crops). The homogenous clones are exact genetic copies of their mother plants, if mutations are ignored. This is more or less obvious in potato, cassava or sweet potato field plots, or in fruit and tree plantations, provided no genotype mixtures are observed. What is not directly obvious to an observer is that each clone line or variety in the field or plantation is a highly heterozygous hybrid (clone lines and varieties are highly heterozygous hybrids comparable with heterozygous hybrids developed in hybrid breeding). It should be noted that due to polyploidy, clonally propagated crops are usually more heterozygous than those diploid crops in which hybrid breeding is applied. The difference between “clone hybrids” and “seed hybrids” such as maize is that the first are propagated by asexual reproduction and the latter are developed by sexual reproduction.

13.3 POLYPLOIDY

General knowledge about polyploidy is required to get an understanding of breeding clonally propagated crops. Polyploidy has a strong effect on the performance of clones as well as the parent–offspring correlations. A polyploid genotype contains more than two homologous sets of chromosomes in the nucleus of somatic cells. According to the number of chromosome sets in the nucleus we distinguish different polyploid types: triploid (three sets; 3x), tetraploid (four sets; 4x), pentaploids (five sets; 5x),

hexaploids (six sets; 6x) (Tate, Soltis and Soltis, 2005) – and species with even higher polyploidy levels are known (Table 13.1). The haploid level (one set; 1x) does not occur as a normal stage in the life cycle of a crop. However, haploid plants occur by spontaneous mutations, wide crosses and anther culture (e.g. diploids are developed from tetraploid potatoes by pollination with specific clones of *S. phureja* and haploids by anther culture). Haploids are occasionally used in FPB of clonally propagated crops, especially potatoes (Hermesen and Verdenius, 1973; Wenzel and Foroughi-Wehr, 1984). In crop evolution different polyploidy levels originated from genome mutations and by hybridization between very closely related species. Autopolyploids and allopolyploids include wheat (*Triticum durum* and *T. aestivum*), canola (*Brassica napus*) and cotton (*Gossypium* spp.), and nearly all clonally propagated species are autopolyploids. The homologous chromosomes in autopolyploids are similar enough that multivalents of the same homologous chromosomes are formed. Doubling of chromosomes occurs if the spindle poles are not developed when the nucleus is dividing chromosomes in mitotic and meiotic cell division. There are several possible outcomes of abnormal meiosis. Natural formation of 2n gametes was most important in evolution of cultivated *Solanum* species, and the formation is mainly determined by one recessive gene (Watanabe and Peloquin, 1988), so this character can be used in breeding potato. Polysomic inheritance is sensitive to disorders and therefore autopolyploids often have reduced fertility, and occasionally they are completely infertile and propagate only asexually.

Multiple chromosome sets occur spontaneously in nature from 2n gametes and can be induced artificially by colchicine (an alkaloid of autumn crocus, *Colchicum*

autumnale). In the case of diploid plants (2x), this leads to tetraploid plants (4x). An example is the evolution of *S. tuberosum* spp. *andigena* (4x) from cultivated *S. stenotomum* (2x) (Hawkes, 1979). Hybridization of diploid and tetraploid plants forms triploid plants (3x) and by a further doubling of chromosomes hexaploid plants (6x) are formed. An example is hexaploid *I. batatas*, which probably evolved by genome mutation and hybridization, because the sweet potato genome (6x) consists of two closely related sets of chromosomes (B₁B₁B₂B₂), of which one is duplicated (B₁B₁B₂B₂B₂B₂) (Shiotani and Kawase, 1989; Austin and Huamán, 1996). Many important clonally propagated crops are triploids (3x), such as the economically important genotypes of banana and plantain (*Musa* × *paradisiaca*). The triploid banana and plantain groups evolved in two different ways by genome mutation and hybridization: in the case of banana, from one diploid wild species *M. acuminata* (AA) to form the triploid banana group (AAA), and in the case of plantain, from two diploid wild species: *M. acuminata* (AA) and *A. balbisiana* (BB), forming the triploid plantain group (AAB) (Simmonds, 1962). Many FVs in the banana and plantain group evolved only by somatic mutation, because triploid banana and plantain are infertile. However, breeding triploids is possible by working with two gene pools, one which is diploid and the other which is tetraploid, such as using gene pools of *M. acuminata* and *M. balbisiana* on a diploid and tetraploid polyploidy level to develop new triploid banana and plantain varieties.

In contrast to autopolyploids, the genome in allopolyploids differs so much between hybridized species that only bivalents of homologous chromosomes of the parental genomes can be formed. The

breeding behaviour of allopolyploids is very similar to diploids. The formation of bivalents or multivalents appears to be genetically determined, e.g. without the gene (ph) on chromosome 5B in polyploid wheat (*Triticum durum* and *T. aestivum*), homologous chromosomes form multivalents. This gene is relatively new in the evolution of wheat (Dhaliwal, 1977). Among clonally propagated crops, cassava (*Manihot esculenta*) is considered to be a diploidized allotetraploid, which also was formed recently in the evolution of plants (Nassar, 2000). Indications for this are: (i) the high chromosome number (2x = 36) of all *Manihot* spp. (other *Euphorbia* have basic chromosome numbers within the range of six to eleven); (ii) natural hybridization occurs among *Manihot* species and crossing barriers appear to be weak; and (iii) *M. esculenta* shows meiotic irregularities, such as terminal non-pairing, multivalent associations and repetition of chromosome types, which results in low fertility of parental combinations.

Polyploid plants usually have larger plant cells, larger and stronger plant organs, greater height and increased biomass production. In nature, polyploid plants tend to succeed in new habitats. In breeding, the tallest and best thriving plants are selected, so that, unintentionally, many crops have been bred to a higher level of ploidy. However, as chromosome number increases, the increase in biomass production becomes successively less, and production decreases above a specific optimum biomass. This optimum differs from species to species. In autopolyploids, this advantage of increased vigour is associated with the disadvantage of increased meiotic disorders during the formation of multivalents. This is the reason why the harvest in many important autopolyploid

crops is represented by vegetative plant parts. Most polyploids display heterosis relative to their parental species, as well as relative to inter-gene-pool crossings within a species. A polyploid population contains three, four, five, six or more alleles at each locus. Hence, considerably more effects due to dominance and epistasis are possible, and the genetic variation due to dominance and epistatic effects in polyploidy crops is very large compared with the genetic variation caused by dominance and epistatic effects in diploid crops. For this reason, the performance of clonally propagated crops is mainly determined by heterosis. Usually in breeding of clonally propagated crops, an F_1 clone hybrid is crossed with another F_1 clone hybrid, so that the offspring shows extremely extensive segregation. In parent-offspring studies it is possible to determine mid-parent and mid-offspring heterosis, as well as the best-parent mid-offspring heterosis (similar to the assessment of heterosis in a hybrid breeding programme of diploid crops—see Chapter 11). In polyploids, more than one allele per locus is transferred in gametes to the next generation, so that, in contrast to diploids, the genetic variation due to dominance determines the response to selection in population improvement as long as the population is not in equilibrium (after recombining parental material in controlled crossings, a population is usually not in equilibrium). In tetraploid potato populations that are not in equilibrium, one-third of the dominance variance is exploitable for selection progress when selection takes place on the female and male sides (Wricke and Weber, 1986; Gallais, 2004). The exploitation of the dominance variance in population improvement, in combination with the selection for different levels of ploidy (using the inheritance of $2n$

gametes), has been proposed for breeding tetraploid potatoes (Ortiz, 1998). Polyploidy, heterozygosity and heterosis make the selection of good parents in population improvement of clonally propagated crops very difficult. A good parent generates large genetic variation around a high family mean. Cross-prediction and inter-gene-pool crosses are very important in population improvement of clonally propagated crops. This aspect of clonal breeding is often neglected and this might be the reason for the low level of breeding progress in many clonally propagated crops. In contrast to population improvement (selection of superior parents – see Section 13.7 below), selection within a given genetic variation for variety development is relatively easy in clonally propagated crops (discard inferior material). All the genetic advantages of clonally propagated crops can be used for variety development, and the genotype finally released is in the hands of the breeder immediately after the initial crossings.

A clonally propagated crop that has no, or nearly no, sexual reproduction is close to a dead end in evolution and breeding. Genetic variability can only accumulate by mutations. However, this source of new variation has often been used to find enhanced types of fruits and ornamentals (van Harten and Broertjes, 1988). Nevertheless, the main source of generating new variation in clonally propagated crops is sexual reproduction. Owing to a more or less regular meiosis in polyploids with an even number of chromosome sets ($4x$ or $6x$), sexual seed production and generation of new genotypes is possible. Nearly all clonally propagated crops, e.g. potato, sweet potato and cassava, are cross-fertilized crops in combination with self-incompatibility. Incompatibility alleles are the reason why specifically sought

after cross combinations are difficult to realize, and seeds from controlled crossings can have a very high value in clonally propagated crops.

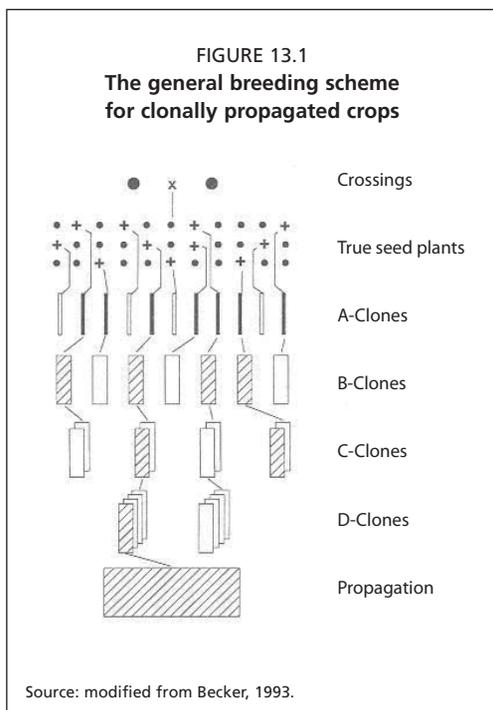
13.4 GENERAL BREEDING SCHEMES

The general principle of breeding clonally propagated crops is to break normal clonal propagation by introducing a crossing step, which culminates in sexual seed production and genetic variation. After the genetic recombination, all subsequent propagation steps are asexual in nature and done by clonal propagation. Nearly all clonally propagated crops are polyploid and cross-fertilized species. A more or less regular meiosis is possible in polyploids, if the number of chromosome sets is even, as in tetraploids (4x) and hexaploids (6x). The parents in cross combinations are highly heterozygous hybrids, with the exceptions of inbreeding lines generated by self-fertilizations or doubled-haploid

and doubled-triploid production. The populations developed from seeds are again formed by very different and highly heterozygous genotypes, which do not exchange genetic material. Each seed plant grown in the so-called seedling nursery can be considered a potentially new variety. This is the basis for selection. The selection between clones is described most often in plant breeding textbooks as a process conducted in several steps (Figure 13.1).

The breeding scheme illustrated in Figure 13.1 is straightforward and it is most often interpreted as requiring clonally propagated crops to be bred sequentially in several steps over several years. The diagram implies that there are two parents being crossed, followed by five subsequent selection steps in time (one selection step in seed plants and four selection steps in clone plants). This is misleading. First the breeder must work with many parents (further details about number and size of crosses are given in Section 13.5). Second, there is no further genetic development in clonally propagated crops as one moves between selection steps. The selected D-clone in Figure 13.1 is genetically identical to the true seed plant the selected D-clone derives from. Provided that the true seed plant can be cloned in large quantities, it is theoretically possible to test the population with adequate accuracy in the first year to select the 'best' genotype.

Selection among true seed plants is made for tolerance and resistance to pathogens. However, often no selection between plants grown from seed is made by the breeder. Nevertheless, natural selection occurs during germination, and should not be completely avoided, because genotypes difficult to germinate delay the breeding programme. The main reasons for no selection in the seedling nursery are: (i) plants grown from



seed often differ considerably from plants raised from vegetative planting material, (ii) the plants raised from seeds are normally grown in pots in greenhouses, and for most traits this is not representative of field conditions, and (iii) a single plant evaluation is usually not appropriate, with the exceptions of susceptibility to highly aggressive pathogens. In field crops, an important factor is interplant competition. A genotype must be tested under conditions that simulate the field conditions in practice. For this reason several plants of each clone are tested in plots in blocks under homogenous field conditions. The aim is an unbiased comparison of genotypes within blocks. The number of plants per plot and the plot size depends on the crop as well as the breeding stage. Fruit trees and perennial shrubs are tested in larger plots with fewer plants than potatoes, and these again are tested in larger plots than cut flowers. Early selection stages (A-clones and B-clones) are tested in smaller plots than later selection stages (C-clones and D-clones). The amount of planting material at each breeding stage is determined by the propagation coefficient of the crop. For example potato has, among clonally propagated crops, a very low propagation coefficient of about ten, whereas sweet potato has a relatively high propagation coefficient of between 30 and 90 (depending on the field propagation method used). This is one factor why potato breeding is relatively slow (about eight to ten years from cross to variety release).

Breeders do not breed for a single environment; they breed for a range of environments. Hence, the field evaluations must simulate the range of target environments. For this reason, and depending on the propagation coefficient, the clones are tested in plots, in homogenous blocks, at several locations and for several

years. It is obvious that the wide range of quality preferences and the numerous pests and diseases in each clonally propagated crop and their interaction with genotypes justifies decentralization and participatory approaches. However, the better simulation of the final target environment realized with FPB justifies a stronger PPB approach. Many advocate PPB because the stress and marginal field conditions of resource-poor farmers are not adequately simulated by FPB (see also below). In this context the two clear advantages of breeding clonally propagated crops should be pointed out: (i) no genetic changes occur in genotypes after seed has been produced; and (ii) the total genetic variation of genotypes (comprising the genetic variances due to additive, dominance and epistatic effects) can be exploited by selection. For these reasons, only the genotype \times environment (G \times E) interaction and the plot error must be considered (and reduced by testing in several environments) to identify the best clone.

13.4.1 Early breeding stages and PPB

In the general breeding scheme (Figure 13.1) each surviving seed plant is cloned to be raised as A-clones in observation plots (visual screening of general clone performance), or evaluation plots (recording of data on specific traits of each clone). Figure 13.2 shows the planting of sweet potato A-clones. The plot size of A-clones is usually a single-row plot comprising 3 to 5 plants. The trial is conducted with no replications. It is open to discussion whether A-clones should be evaluated at two locations. Selection theory results show that it is nearly always the best resource allocation to test as many clones as possible at one location, without replications (Wricke and Weber, 1986). Many breeders use only one location at the

FIGURE 13.2
Planting early selection stages of sweet potato for the
accelerated breeding scheme in San Ramon (one of four locations)



early breeding stages due to the restrictions of the propagation coefficient and breeding budget. However, there are several reasons to test A-clones at two locations: (i) a trial at one location can be lost (e.g. extreme weather conditions) and then a full breeding step and population is lost; (ii) trials at only one location are of little value (the $G \times E$ interaction cannot be separated from the genotypic effect); and (iii) the response to selection is still very close to the optimum in a wide range of scenarios, including the scenarios where A-clones are tested at two locations (Grüneberg *et al.*, 2004). Moreover, information from contrasting environments can be combined if the breeder tests A-clones at two locations. For example, clones that clearly fail in

a marginal or hot-spot environment (for drought, salinity, biotic challenge, etc.) can be discarded, or at least considered with caution in good environments.

A-clones are only selected for highly heritable traits such as general performance (growth type; tuber, root or fruit size, shape and colour), resistance to pests and diseases, harvest index, dry matter and nutritional quality. Breeders nearly always conduct a visual selection at the A-clone breeding stage. However, it can be questioned if the A-clones selected by the breeder match farmer needs and would be selected by farmers. With two locations, one location can be easily evaluated by farmers in a PPB approach, while the other location is used by the breeder. It should be noted

that visual selection of general performance can also be an efficient indirect selection for yield. In sweet potato, we observed among several thousand A-clones grown in 1 m-row plots at three locations a heritability for yield of about $h^2 \approx 0.4$ (harvesting and recording all A-clones for yield at all three locations). It was considered as ‘useless work’, because a visual selection at the first location resulted in a nearly common set of selected clones and a heritability for yield of about $h^2 \approx 0$ in the selected fraction. This was demonstrated for two different breeding populations grown in two different seasons, so that the breeding scheme was changed. Only those clones that have passed the visual selection step at location 1 are harvested and considered for storage root quality evaluations at location 2 and 3. However, relying on visual selection in early breeding stages requires a person who is very experienced with sweet potato. We think farmer participation at the visual selection stage in early breeding stages is essential to avoid genotypes entering later breeding stages with characteristics (storage root size, shape, form, colour, etc.) unacceptable to farmers. As described above, farmer preferences vary substantially both within and between regions, and the visual selection can be conducted by independent farmer groups. The advantages of PPB are very obvious in the early selection stages of clonal breeding, in which large numbers of fixed genotypes must be screened for many highly heritable traits. PPB in the early selection stages has been successfully applied in potato (Gabriel and Torrez, 2000), cassava (Manu-Aduening *et al.*, 2006) and sweet potato (Gibson *et al.*, 2008), and by working with two or three locations it can be linked into FPB, in which selection is conducted for traits that cannot be evaluated by farmers, such as

nutritional quality (starch, vitamins and micronutrients by fast through-put analysis methods) (Hartmann and Buning-Pfaue, 1998; Lu, Huang and Zhang, 2006; Zum Felde *et al.*, 2007; Bonierbale *et al.*, 2009).

In the next season, B-clones—also called “promising clones”—are planted in larger plots in 2 to 3 rows with planting material obtained from selected A-clones. The B-clone trials are still conducted without replications, but generally at two or more locations. The B-clone stage is usually the beginning of selection for low heritability traits such as yield, biomass and yield stability. The determination of stability parameters such as the slope of the regression line and deviations from regression (Fox, Crossa and Romagosa, 1997) requires at least three locations. However, it should be noted that stability parameters from less than 6 environments are still of little value. As mentioned above, a strong justification for PBB is that stress and marginal field conditions of resource-poor farmers are not adequately simulated by FPB (Ceccarelli, 1994). Cross-over G×E interactions occur, and what appears to be good in resource-rich environments often does not perform well in resource-poor environments. This has also been clearly observed in sweet potato, and outstanding clones for resource-poor environments were discarded by FPB (e.g. the clone SR92.499-23; Grüneberg *et al.*, 2005). Usually, but not always, the response to selection in poor production environments is smaller than in good production environments. The genetic variance is smaller while interaction and error are larger, so that the performance of individual clones becomes more difficult to distinguish. However, outstanding genotypes with different growth types adapted to resource-poor environments cannot display their full potential if FPB

does not test in such environments. Taking sweet potato breeding as an example again, yield stability is associated with harvest index (Grüneberg *et al.*, 2005). Under drought stress, good performing sweet potato clones have a harvest index of about 0.5 (on the basis of fresh matter storage root yields and total fresh matter biomass yields). Vine production is of considerable importance to farmers to obtain sufficient planting material for the next growing season. Clones performing well in resource-rich environments usually fail in drought-stress environments due to insufficient vine production rather than to unacceptable storage root production. At the same time, outstanding clones in drought-stress environments show a strong increase in vine production with medium storage root yields when grown in environments with good water supply (Andrade, unpublished). The selection of genotypes with desired growth types or desired sink–source allocations in marginal environments requires that breeders evaluate the breeding population in such an environment; this characteristic cannot be determined in a resource-rich environment. Here we suggest linking the evaluation in a marginal environment with the visual selection in early breeding stages. All clones that fail in the marginal environment (i.e. extreme reduced storage root production or vine production) are eliminated from all other selection steps.

13.4.2 Later breeding stages and PPB

At the beginning of the C-clone and D-clone selection stages the breeding population has been reduced to between 30 and 300 clones. While the number of clones in later selection stages is further reduced, those selected clones are tested in more environments and in replications. The plots for C-clones and D-clones are

3- to 5-row plots. All important agronomic traits are determined, including taste and post-harvest characteristics. Furthermore, it merits determination of the above-mentioned stability parameters: (i) slope of the regression line, and (ii) deviations from regression, as well as conducting an Additive Main Effect and Multiplicative Interaction (AMMI) Analysis in those cases where the regression model does not fit (Fox, Crossa and Romagosa, 1997). Usually, a clone is considered to have stable performance if the slope of the regression line is close to 1, and the deviations from the regression line are small. An important question in later breeding stages is that of how many locations and how many replications to use. With more locations and more replications, the estimation of the yield performance of clones is more reliable. At the same time, for a given testing capacity, increasing the number of locations and replications results in fewer clones being tested. Generally, the gain from increasing the number of replications is less than that obtained by increasing the number of genotypes and locations. Investigations of this problem in selection theory have led to a recommendation to conduct advanced clone trials still with no replications but in the maximum number of environments that can be managed by the breeder (Utz, 1969, cited in Wricke and Weber, 1986). However, many scientists are still very reluctant to conduct trials without replications. Since the fixed costs of experimental stations are high, it is usually an advantage to (i) create ‘artificial environments’ on experimental stations (by running part of a station without fertilizer or with less irrigation) and (ii) to go on-farm to evaluate clones with farmers, i.e. PVS. However, nearly all of the initial genetic variation in the breeding population has been discarded at later breeding stages,

so that specific characteristics needed by farmers and consumers are often no longer present in advanced or elite clones if they had not been considered at earlier breeding stages.

13.5 MODIFICATIONS OF THE GENERAL BREEDING SCHEME

The general principle for breeding clonally propagated crops presented above is very simplified. In practice, it is more or less modified. The differences can be large, depending on the crop, country and breeder. For example, resistance or tolerance can already be determined at the true-seed plant stage by eliminating infected plants from the seed nursery. Potato breeders usually try to obtain only a single tuber from each true seed plant to start selection with single plant tests. Clone selection in shrubs and fruit trees uses fewer plants per row and fewer selection stages. Potato breeding uses more selection stages due to the low propagation coefficient of potato. However, there is a common question in all the different breeding schemes: How many genotypes should be selected at each selection stage? In selection of breeding clonally propagated crops this can be easily determined using selection theory. There is an optimum number of clones, locations and replications at each selection step for a given test capacity. Fortunately, the area around the optimum is flat and deviations from the optimum do not have large effects, as long as the deviations are not strong. To select between 5 and 20 percent of the total number of clones at each step is still close to the optimum. However, in the wide range of practical breeding situations, the optimum has always been found in the direction of higher selection intensities, more so than most breeders intuitively realize. It is important: (i) to increase the

number of genotypes at the first stage, to the maximum of the available breeding capacity; (ii) to use a high selection intensity; and (iii) to use as many environments as can be managed at each breeding stage (Wricke and Weber, 1986). Replications are of minor importance and should only be used at the final breeding stages. These characteristics of the optimum in multistage selection for clonally propagated crops led to the suggestion of using an accelerated breeding scheme (ABS) for clonally propagated crops in sweet potato breeding (Grüneberg, unpublished).

ABS responds to the frustration that it takes on average seven or eight years from a cross until variety release. Donors are also reluctant to invest in breeding when concrete outputs take so long to materialize. ABS uses the simple fact that in breeding clonally propagated crops each true seed plant is already a potential variety, with the advantages of sweet potato having a very short crop duration (3 to 4 months) and a high propagation coefficient (up to 90 cuttings per plant within 3 to 4 months). ABS overturns the general principal breeding scheme of clonally propagated crops by: (i) crossing and multiplication; (ii) early selection stages; and (iii) late selection stages. Everything that can be implemented simultaneously in these three stages and years is done simultaneously in different environments. However, to reduce labour, every clone that has not met a desired target for a character in the first environment is discarded and not considered (harvested) in the second environment, and the same for characters evaluated in the second environment, and so forth. In selection theory, this multi-trait selection procedure is designated 'independent culling' and it is the procedure also used to optimize multistage selection procedures (Cochran,

1951; Wricke and Weber, 1986). In ABS, independent culling is conducted: (i) in a poor resource environment where clones undergo visual selection; (ii) only those clones passing the first selection step are harvested in environments 2 and 3 to determine yield and quality of selected good performance clones over all traits and environments (index values are determined by the Pesek-Baker index (Pesek and Baker, 1969) to assist the breeder in their selection decisions); and (iii) only those clones that have passed the second selection step are harvested in environment 4, where clones were already planted in season 2 in a farmer's field under high SPVD pressure in a third selection step to select for SPVD tolerance. About 300 sweet potato clones enter the later breeding stages. In two subsequent seasons and two selections steps, 4 to 5 clones are finally selected for variety release (first season: 300 clones, three environments, two plot replications and 5-row plots; second season: 40 clones, 16 environments, two plot replications and 5-row plots). This is carried out in cooperation with NARS and farmer groups.

13.6 MAINTAINING VARIETIES AND S-CLONE MULTIPLICATION

As a result of clonal propagation, maintaining varieties should not be difficult. Genetic changes in varieties do not occur by undesired crossings nor by segregation, and mutations are rare. However, the opposite is the truth, and maintaining clonally propagated varieties is a difficult and expensive part of the breeding operation. The main reason is that in clonal propagation through vegetative plant parts, many more diseases can be transmitted compared with seed propagation. A new variety will have no impact in practice, and even can be lost (a clone hybrid developed

from two hybrids cannot be reproduced by crossing the hybrids again) without a system that maintains and provides at least some healthy planting material.

Numerous viruses, bacteria and fungi are transmitted by vegetative planting material. Viruses are particularly important, because viral diseases cannot be controlled chemically. Viruses are spread by vectors, most often aphids and whiteflies. The traditional maintenance of varieties and production of healthy planting material includes protecting the base plants of varieties in greenhouses or under nets, and to prevent the development of a vector population by intensive use of insecticides. The base material is also termed 'mother plants'. However, under these conditions, only 20 to 200 plants of each variety can be maintained, and planting material must be produced in the field. These clones in the field for producing healthy planting material are the so-called S-clones, because planting material is usually called seed in clonally propagated crops. Healthy S-clone production is supported by (i) application of insecticides against vector populations (monitoring by yellow cards); (ii) choosing locations for S-clone production that are out of range of vector populations (i.e. locations close to the sea or in cool highlands); and (iii) removing all visibly infected plants from S-clone fields.

The detection of virus infections has been simplified by use of the enzyme-linked immunosorbent assay (ELISA) procedure. The principle is a reaction between the viruses in plants and antibodies against these viruses. The reaction is made visible by an enzymatic colour formation. In practice, some leaf sap is pressed out and the colour reaction is assessed on special test plates coated with antibodies. In the case of sweet potato, the plants tested negative for viruses

are further grafted on an indicator plant such as *Ipomoea setosa* to confirm the absence of viruses for sweet potato viruses. In this way all maintained mother plants of a variety are routinely screened, and only virus-free mother plants are used for further propagation steps. Recently, techniques have been developed to detect viral DNA and RNA directly by real-time polymerase chain reaction (PCR) (Mumford *et al.*, 2006).

However, the best option for maintaining clone genotypes is to start from absolutely virus-free material. This is obtained by *in vitro* propagation of plants under sterile conditions, and these *in vitro* plantlets are the starting point for greenhouse and field propagation. *In vitro* plantlets are replacing mother plants in the greenhouse, often by eliminating all greenhouse plants. If no virus-free material is available, new virus-free plantlets can be obtained by chemotherapy and meristem culture. Meristems of very-fast-growing infected plants are virus free following proper heat treatment, because viruses only start to enter older plant cells. However, this process requires considerable time (at least 18 months for sweet potato, and depends on the virus titre of the infected source plants). In breeding, virus-free material can be achieved by germinating true seed *in vitro* and maintaining these true-seed plantlets *in vitro* until the final selection decision has been made.

Distribution channels for clonally propagated crops are well developed in temperate regions of the world. However, they are almost non-existent in most tropical and subtropical countries, although the pest and disease pressure is considerable higher than in temperate regions. S-clone production in resource-poor environments is nearly all in the hands of farmers, and the health status of planting material is a key factor in high farm yields. Without a

certain discipline in S-clone production on farm, the yield level remains low, although virus-tolerant varieties with good overall performance are available. The most important factors for S-clone production on farm are: (i) separating S-clone production from cultivation for production; (ii) removing all visibly infected plants in S-clone field areas; and (iii) obtaining new, healthy planting material at least occasionally from private or public sources. Nevertheless, the private and public seed sectors are an important factor in production of clonally-propagated crops, but this topic belongs to integrated crop and pest management (Salazar, 1996). The breeder's role in this context is to maintain and provide virus-free starter material for the private and public seed sectors.

13.7 SELECTION OF PARENTS AND PREDICTION OF CROSS OUTCOMES

The choice of parents is perhaps the most important step in a breeding programme. Many breeders make several hundred crosses each year and it is often observed that in later steps of the breeding programme the best clones derive from one or only a very few crosses. Hence, there is a desire to predict which cross combinations are most promising. If this were possible, the efficiency of a breeding programme could be increased by reducing the number of cross combinations and increasing the number of genotypes from good cross combinations (produce more genotypes from within the best families). In the situation where not much is known about the performance of a cross, the number of combinations should be increased to the maximum of the breeder's capacity and the number of genotypes per cross should be kept small. The rationale underlying this is based on selection theory, which shows that if "the breeder has no

prior knowledge on the cross ... the breeder has to make as many crosses as possible”, which is also minimizing the risk of raising genotypes with poor performance (Wricke and Weber, 1986). As mentioned above, most clonally propagated crops are polyploid and highly heterozygous, so that dominance and epistatic effects contribute considerably to clone performance. For this reason, it should be assumed that not much is known about the value of a cross combination until it has been made and tested. This is in agreement with our observations in sweet potato, where the correlation between mid-parent and mid-offspring yields is low ($r \approx 0.5$). We currently recommend raising 10 to 20 genotypes per cross combination, while increasing the number of cross combinations to the maximum possible with the resources available. However, after clones of these crosses have been evaluated, the good crosses should be repeated on a large scale. An optimum for the number and size of crosses can be determined if estimations are available for the genotypic variance between crosses and within crosses, and the non-genetic variance components (Wricke and Weber, 1986). Breeders often generate a large number of seeds in polycross nurseries, but in these only the female parent is controlled. The correlation between parent and mid-offspring in breeding populations derived from polycross nurseries is half of mid-parent–mid-offspring correlation in controlled crosses.

Often the parents are chosen due to their performance *per se*. For theoretical reasons, this cannot be very secure in clonally-propagated crops. Clone varieties are highly heterozygous hybrids and usually polyploids, so that segregation in crossings is almost unpredictable. Therefore, for a long time now, suggestions have been made for better assessment of parents; however, they

are rarely used in practice. One suggestion is to determine the value of a parent on the basis of the offspring performance from test crosses. Another suggestion is to work on a reduced polyploidy level, which has been especially proposed for breeding tetraploid potatoes (Ross, 1986). However, the latter has been little applied in practice for parental selection, but has often been used to incorporate germplasm of wild *Solanum* species into advanced breeding populations (Tarn *et al.*, 1992). Parental selection on the basis of test crosses are made on a large scale in potato breeding programmes for long-day, temperate climates (150 to 500 cross combinations per breeding programme, cited by Ross, 1985). It has been observed that specific combining ability is nearly as large as general combining ability, and in some cases specific combining ability has been observed that is clearly larger than general combining ability (Sanford, 1960; Mullin and Lauer, 1966; Tai, 1976; Killick, 1977; Veilleux and Lauer, 1981; Gaur, Gopal and Rana, 1983, cited by Tarn *et al.*, 1992; Gopal, 1998; Kumar, 2004; De Galarreta *et al.*, 2006). This is not surprising as long as potato breeders do not work with two clearly separate gene pools for variety development. In potato breeding for tropical and subtropical regions, heterosis and high general combining ability have been observed between *andigena* and *tuberosus* gene pools in tuber-propagated potatoes and in true-seed potatoes (Enrique Chujoy, pers. comm.). However, as long as these gene pools are not improved on the basis of general combining ability separately from the complementary gene pool, such effects cannot be exploited in the long term.

In sweet potato experiments we observed a mid-parent–mid-offspring heterosis of 84 percent among 48 cross combinations (or 184 percent if the mid-parent value is set to

100 percent). This is a clear indication that the design of breeding schemes using the combining ability of two gene pools merits investigation. Two breeding gene pools are available for sweet potato to test heterosis: the Jewel Gene pool, developed mainly from North American varieties, and the Zapallo-SPK Gene pool, developed mainly from South American and African FVs.

The value of a parent is nearly always determined by several characteristics. In general, parents should be recombined with a good combining ability and good performance over all traits. The PPB study in Uganda (Gibson *et al.*, 2008) underlines how many characteristics are important for good performance over all traits. Moreover, FPB also has the aim of improving nutritional quality, especially pro-vitamin A, iron and zinc concentrations (Pfeiffer and McClafferty, 2006) in potato, sweet potato, cassava, plantain and other crops. With an increasing number of characters, breeders operate with larger breeding populations, as in potato and sweet potato. Aiming at only 30 genotypes finally selected, and assuming 10 characters each, selected in sequential selection steps with a selected fraction of ten percent (1 out of 10), then 300 000 000 000 genotypes would be needed in the original base population. Populations of this size cannot be established in practice. Moreover, even if the population size is extremely large, some desired combinations probably do not exist, such as sweet potato genotypes with high yield, high SPVD tolerance, high DM and high pro-vitamin A, iron and zinc concentrations). Often, breeding can only approach the desired genotype in several steps of recombination and selection. In practice, some characters are selected sequentially (especially where there is clearly a lowest acceptable value (tuber size, shape and

colour, as well as pest and disease resistances), while others are selected simultaneously by aggregating characters into an index (often an intuitively formed index, such as score values for overall performance).

A parent appears to have a good overall trait performance if no trait is below the population average. However, only in those cases where trait associations are close to zero or positive can it be expected that parents with good performance over all traits produce offspring in which each character has been improved. In parental selections, negative trait associations can be very critical. Table 13.3 gives an example for sweet potato, in which DM shows a strong negative trait association with pro-vitamin A, iron and zinc concentrations, as well as a moderate negative trait association with storage root yield. The associations in the example are strong enough that under various scenarios of multi-trait selection the breeding population is improved for yield, pro-vitamin A, iron and zinc, whereas the DM of the population decreases.

In other words, the DM is changing in the wrong direction even though it was selected for improvement. These surprising undesired effects in the case of sweet potato and DM improvement in connection with pro-vitamin A, iron and zinc improvement was also observed for the Williams selection procedure and this index selection procedure (Williams, 1962) comes very close to intuitive selection procedures used by breeders in which a weight is assigned to each trait on the basis of its economic importance. The only selection procedure that can monitor the response to selection in each trait is the Pesek Baker index (Pesek and Baker, 1969). However, this index requires estimations of genetic variance and co-variances, but the procedure ensures that parents are selected that

TABLE 13.3

Estimations of genetic correlations for yield, dry matter, total carotenoids, iron and zinc in sweet potato storage roots of 24 megaclones and 26 advanced breeding clones grown in at two locations in two replications

	Storage root yield	Dry matter	Total carotenoids	Iron
Megaclones (orange and white fleshed)				
Dry matter	-0.49			
Total carotenoids	-0.06	-0.54		
Iron	-0.26	-0.23	0.94	
Zinc	-0.22	-0.39	0.93	0.74
Advanced breeding clones (only orange fleshed)				
Dry matter	-0.54			
Total carotenoids	0.55	-0.71		
Iron	-0.24	-0.07	0.14	
Zinc	0.39	-0.20	0.37	0.53

develop populations in which traits are improved according to a ratio of desired genetic improvements (so-called desired genetic gains) given by the breeder.

An alternative is the Elston index (Elston, 1963), in which the breeder can raise the threshold for the trait at risk by modifying the lowest acceptable value for each. This index can be easily applied in each replication and environment, so that index mean values for each genotype can be calculated together with other statistical parameters (Grüneberg *et al.*, 2005).

We are aware of only one case in which PPB has been applied for the selection of parents in clonally propagated crops. In the Cochabamba region of Bolivia, farmers selected potato parents in an *andigena* population, which had been improved for agronomic performance and Late blight tolerance. Selected clones in this population were used as parents with the regionally grown FV 'Waycha' (Gabriel and Torrez, 2000) and the PPB approach included hand-crossing by farmers. We think that the ability of farmers in the selection of parents is limited beyond a selection of clone performance *per se*. Test crosses, general combining ability, specific

combining ability and improving gene pools on the basis of general combining ability values (called reciprocal recurrent selection in maize breeding) are the most difficult tasks in breeding; however, they can greatly increase yield gains. At the same time, we think that the visual selection of potential parents in a PPB approach should be used as additional information by the breeder. It should be noted that the work plan for both the selection of parents for the next cycle of selection and the early selection stages for variety development are always to a certain extent in common. In sweet potato breeding at CIP we use a combination of sequential and simultaneous index selection in early selection stages (see also above): (i) visual selection by eliminating all genotypes that do not meet the lowest acceptable values for each trait (this lends itself to PPB); (ii) in the remaining selected fraction (about 2 500 clones), apply index selection for yield and nutritional quality traits using the Pesek-Baker index, with the square roots of variance components as desired genetic gains; and (iii) selecting for pest and disease tolerance (mainly SPVD) in the remaining selected fraction (about 300 clones) by visual selection (this lends itself to PPB) and

ELISA. The remaining 100 to 200 clones enter later breeding stages, but are also used as parental material for the next cycle of recombination and selection. In such a breeding system, with one population, two PPB steps can easily be applied. However, a PPB approach is feasible also in inter-pool crosses linked with general combining ability improvement. Farmers select in families (derived from recombining the two gene pools) in early generations for variety development (as described above). The interesting information for the breeder provided by farmers could be the numbers of selected clones per family. With this information the breeder can focus only on those parents in the improvement of the separate gene pools, which for the farmer results in interesting cross combinations with the other gene pool. On top of this, the breeder can use the opportunity to apply the general combining ability concept. This would be a very elegant PPB approach for selection of parents and cross prediction. Although Hull (1945), in his fundamental paper on reciprocal recurrent selection, proposed this for breeding clonally propagated crops, this method of clonal breeding is rarely found in practice.

The topic has been considered in breeding clonally propagated trees (e.g. Baudouin *et al.*, 1997; Kopp *et al.*, 2001; Pâques, 2004) and recently discussed by Miles (2007) in the frame of apomixis for cultivar development in tropical forage grasses. The proposed “evolutionary breeding approach” for *Musa* spp. (Ortiz, 1997) is also in the narrow sense a reciprocal recurrent selection scheme. However, subsequent application of reciprocal recurrent selection is rarely found in practice, although we think that this is the way ahead to exploit heterosis and achieve more breeding progress in clonally propagated crops.

13.8 APOMIXIS

As mentioned earlier, the principle advantage of breeding clonally propagated crops is that each clone variety is fixed and maintainable. However, this is associated with the disadvantage of vegetative propagation. Diseases are easily transmitted and the maintenance of varieties and the production of healthy planting material are expensive. The ideal propagation system for clone varieties would be vegetative propagation by seeds. This ideal propagation system exists in nature, and is called apomixis (Nogler, 1984). Apomixis is the formation of seeds without meiosis, and two forms are distinguished: (i) agamogenesis (also called gametophytic apomixis), in which the asexual embryo is formed from an unfertilized egg; and (ii) adventitious embryony, in which the asexual embryo is formed from nucellus tissue. Apomictically produced seeds are genetically identical with the parent plant. The breeding work on apomictic species is very difficult and requires developing population improvement by sexual reproduction and subsequent variety development by apomixis. Apart from some forage (Miles, 2007) and citrus species (Soost and Roose, 1996), apomixis is not used in plant breeding.

The difficulty in breeding apomictic crops is the development of genetic variation. However, in populations with a high frequency of apomictic plants, both facultative apomicts and completely sexual plants can usually be found, and such genotypes can be used to develop new genetic variation. For breeding, it is important to find or develop a system in which both apomixis is maintained (variety development) and sexual reproduction is restored (population improvement) so as to be able to develop new genetic variation. This can be compared to male sterility

systems used in hybrid seed production. It is interesting that apomixis is distributed across many plant families. It appears not to be controlled by a complex genetic system. An example is Guinea grass (*Panicum maximum*), in which the sexual tetraploids are recessive homozygous (aaaa), whereas apomictic genotypes carry a dominant allele and are heterozygous (Aaaa) (Savidan, 1983). So far, studies on apomixis have been mainly made in tropical grasses, but more and more attention is being paid to rice and maize. There are opinions that apomixis systems will become available to breeders, and in this context gene isolation and an 'apomixis gene' have been mentioned (Savidan, 2000). However, so far there is no such apomixis system usable in breeding programmes. The major problem is that plants with the same genotype can express different degrees of apomixis.

13.9 PROPAGATION OF POTATOES BY SEED

Finally, the option that clonally propagated crops can be propagated by sexual seeds is considered. In many countries there have been research projects in which potatoes were cultivated by seed. These are potatoes that are sown instead of planted. Since the planting material of clonally propagated potatoes is often called a 'seed' potato, the term 'true potato seed' (TPS) was introduced. The use of TPS has two principle advantages: the most important potato diseases cannot be transmitted in true seed, and only a few hundred grams of TPS are needed to cultivate a potato field, where usually several tonne of tubers are needed (Simmonds, 1997). This is associated with two disadvantages: potatoes grown from seed are weak in vigour and are sensitive to many factors, and the breeding method and advantages of breeding clonally propagated crops can

no longer apply. Moreover, breeding TPS potato as a cross-fertilized crop will not lead to completely homogenous varieties. This is the reason why only a few TPS varieties have been developed in the Northern Hemisphere. All these have been exclusively used for home garden production. However, we think that by using hybrid selection schemes and inbreeding in two separate gene pools it should be possible to develop more and more homogenous and attractive TPS varieties.

The advantages of TPS are mainly of interest in tropical and subtropical regions of the world. Under these climatic conditions, the production, storage and transportation of potato planting material is difficult. Moreover, potato yields are considerable lower in tropical and subtropical regions of the world than in the Northern Hemisphere, so that about 20 percent of the harvest is needed as planting material. Hence TPS varieties in the tropics can have 20 percent lower yields compared to clonally propagated potato varieties and remain competitive. About 20 TPS varieties have been developed. Most interesting are those varieties developed from recombination of the *andigena* and *tuberosus* gene pools. However, the original idea of raising seedlings in nurseries and then planting seedlings into the field by hand has not been adopted. What has been adopted is to raise TPS varieties in seedling nurseries to obtain healthy planting material, and then to cultivate these TPS varieties for several growing seasons as a clonally propagated crop, and to request true seed again after yield declines are significant due to declining health status (Fuglie, 2001). However, today, not more than 10 000 ha of TPS are grown, mainly in Asia, which trace back to about eight TPS varieties. The future of TPS is debatable. From the breeding perspective,

the future of TPS will mainly depend on working with two gene pools, in which a certain extent of inbreeding is applied, with subsequent use of general combining ability to improve these two gene pools.

13.10 POTATO

Breeding potatoes has been reviewed by Tarn *et al.* (1992). The andigena potato (*Solanum tuberosum* subsp. *andigena*; autotetraploid with 48 chromosomes) originated in the highlands of South America about 5000 BC, while today two-thirds of world potato production is in temperate latitudes. Following introduction into Europe, andigena evolved into the Irish potato (*S. tuberosum* subsp. *tuberosum*), which is mainly characterized by day-length neutrality, uniformity of tuber shape, shorter crop duration and higher harvest index than andigena. Andigena remains the predominant cultivated potato in the Andes, whereas the Irish potato is the potato of commerce in long-day temperate climates. Potatoes introduced into other, tropical, regions of the world trace back to breeding populations derived from crossings between andigena and Irish potato. However, in the Andean region, seven other potato species are still in cultivation; most important are phureja (*S. phureja*; diploid with 24 chromosomes), limeña, ajanhuri and rucki. In addition to these cultivated species, 160 wild potato species are known (Hawkes, 1979 and 1981; Spooner and Hijmans, 2001), so that potato might have the largest gene pool among crops. Wild and indigenous species are important resources of pest and disease resistance for andigena and Irish potato. The evolution of the potato was described in the introduction of this chapter. Asia and Europe are the world's largest potato producing regions, with annual production of about 130 and 128 million tonne, respectively, followed by

the Americas (41 million tonne) and Africa (16 million tonne) (FAO, 2006). The top 20 potato producing countries are China (22 percent), The Russian Federation (12 percent), India (8 percent), Ukraine (6 percent), United States of America (6 percent), Poland (3 percent), Germany (3 percent), Belarus (3 percent), Canada (2 percent), France (2 percent), United Kingdom (2 percent), Turkey (2 percent), Netherlands (1 percent), Bangladesh (1 percent), Brazil (1 percent), Romania (1 percent), Peru (0.8 percent), Spain (0.6 percent), Nepal (0.5 percent) and Pakistan (0.5 percent).

Breeding objectives

Characteristic of potato breeding is the large number of breeding objectives. For the Irish potato, quality traits are at least as important as yield. Moreover, breeding for resistance against numerous pest and diseases, e.g. numerous viruses (potato leaf-roll virus (PLRV), Potato virus Y (PVY) and Potato virus X (PVX)), Late blight (*Phytophthora infestans*), dry rots (*Fusarium* spp.), soft rot and blackleg (*Erwinia* spp.), cyst-forming nematodes (*Globodera rostochiensis* and *G. pallida*) have major importance in long-day temperate as well as in tropical temperate climates. For the andigena potato, these pests and diseases are of nearly similar importance (i.e. late blight can destroy the whole crop in cool, high-altitude regions, especially when the weather is wet).

There are clear differences between tropical temperate and tropical hot climates. At temperatures above 25°C, Late blight and cyst-forming nematodes decline rapidly in importance, but Early blight (*Alternaria solani*) and root-knot nematodes (*Meloidogyne* spp.) take over, and Bacterial wilt (*Pseudomonas solanacearum*) is widespread in tropical

lowlands. The phureja potato (for PVY and Late blight) and the wild species *S. acaule* (for PLRV, PVX and both *Globodera* spp.) and *S. demissum* (for PLRV, PVY, and late blight) are important resources in breeding for tolerance and resistance. It should be noted that the pests and diseases presented represent only the most important species. Ross (1985) provides a list of resistance sources in wild potato species.

However, it is possible to find tolerance or resistance genes in cultivated and wild potatoes against nearly all potato diseases. An exception is Bacterial wilt, for which so far no useful tolerance or resistance have been found for breeding purposes. Today, all new Irish potato varieties contain one or more resistance genes from wild and other cultivated potato species. For the Northern Hemisphere, yield, crop duration, tuber size, shape and flesh colour, eye depth, starch content, storability, cooking characteristics, taste and suitability for mechanical harvesting, as well as processing characteristic for chips (crisps) and French fries (chips) are the most important quality breeding objectives. For tropical regions, yield, regional adaptability, crop duration, storability, cooking characteristics, taste and nutritional quality are the most important quality breeding objectives. Outside of the Andes, crop duration is one of the most important traits (i.e. in south-west and central Asia there is a requirement for potato varieties with less than 80 days crop duration). Recently, focus has been given to improve pro-vitamin A, iron and zinc concentrations in tubers to alleviate micronutrient malnutrition in tropical regions (potatoes have comparatively high iron and zinc concentrations). This has resulted in a separate breeding programme for phureja, which has the highest iron and zinc contents among potatoes, together

with considerable levels of total carotenoids, including pro-vitamin A.

Breeding methods

Crossing is relatively easy. In nature, crossings occur easily by open pollination by insects. For breeding purposes the flower architecture of the potato allows easy emasculation and controlled hand pollination. A fruit with about 200 seeds develops from each successful pollination. In commercial breeding, controlled crossings are usually made (both parental genotypes are clearly defined). Genotypes with good performance over all traits and with a certain degree of genetic distance are recombined. The value of a cross combination is usually determined in test-crosses with 100 to 200 seeds per combination. Occasionally plant breeding text-books recommend combining parents with complementary traits. However, many breeders find that this results in potatoes breeding in a 'wild' segregation, so that finally only genotypes can be selected with moderate performance over all traits. Each year, breeders plant 10 000 to 200 000 seeds, which trace back to 150 to 200 cross combinations. Crossings are made with flower sprouts obtained from cuttings of field plants, grown in greenhouses in nutrient solutions. Frequencies of successful crosses differ tremendously between parental combinations and about one-eighth to one-quarter of all parental combinations cannot be recombined due to no flowering, low pollen quality, no fruit formation or genetic incompatibility. For an overview of overcoming crossing barriers in potatoes, the reader is referred to Jansky (2006).

Pre-breeding crosses are important when one requires to improve one or two traits in an enhanced breeding gene pool (e.g. shorter crop duration). Pre-breeding

is usually made in two or three cycles of recombination and selection in which the desired traits are incorporated in a genetic background that is more close to the enhanced breeding gene pool. This is generally done for resistances genes from a wild parent or exotic variety. It often involves an additional selection step at a different ploidy level. The re-synthesis of tetraploids by mitotic duplication of diploid genotypes (colchicine treatment of seed, axillary buds, tuber germs, leave explants or callus) is usually not recommended, because mitotic tetraploids have considerably lower yields than meiotic tetraploids. Meiotic tetraploids occur naturally in crossings between tetraploid and diploid potatoes ($4x \times 2x$) due to meiotic anomalies that result in unreduced gametes (Rowe, 1967; Jacobsen, 1980).

Breeding potato for tropical regions of the world aims mainly at improvement of four gene pools: (i) the andigena (A) gene pool for short-day high altitudes; (ii) the andigena \times tuberosus (AT) gene pool for short- and long-day temperate regions, with emphasis on selection for Late blight tolerance and PVY and PLRV resistance; (iii) the tuberosus \times tuberosus (TT) gene pool for short- and long-day warm regions, with an emphasis on selection for short crop duration; and the (iv) phureja gene pool (P), with emphasis on nutritional quality. In the A, AT and TT gene pools at CIP about 60 parents are recombined by controlled crossings to raise about 20 000 seedlings, whereas in the P gene pool the number of recombined parents is considerable lower (about 30 parents). The selections start in seedling populations for both resistance and tuber formation. In three selection steps the material is reduced to about 300 clones, which are evaluated in 2-row plots with two replications. Later selection stages

include evaluation at several locations in replicated plots. However, the propagation coefficient in potato is very low (≈ 10) so that it takes about eight to ten years before final selections enter the variety release and dissemination stage.

Today there is little investment in TPS in the original sense. However, selection of families that are to a certain degree homogenous in crop duration, tuber form and shape, with some genetic diversity in tuber yield and specific adaptation, are of interest. The reason is that these can be disseminated as seeds and farmers have the option to exploit genetic variation for specific adaptation in a PPB approach. PPB has been successfully applied in Bolivia in early breeding stages (Gabriel and Torrez, 2000) and in later breeding stages (FVS) in Ecuador (Bonierbale, pers. comm.).

13.11 SWEET POTATO

Breeding sweet potatoes has been reviewed by Martin and Jones (1986), Laurie and van den Berg (2002) and Grüneberg *et al.* (2009). The sweet potato (*Ipomoea batatas*, Convolvulaceae, hexaploid with 90 chromosomes) is also known as *batata*, *camote* or yam (United States of America). The crop was domesticated in tropical America about 6000 BC and reached the Pacific and south-east Asian islands naturally or by early seafarers before Columbus. The number of wild species in the genus *Ipomoea* is large (more than 500 species). However, no wild form of *I. batatas* has been found. It is assumed that *I. batatas* developed from an interspecific cross between a diploid and a tetraploid *Ipomoea* species in the *I. trifida* complex. It is possible to re-synthesize new *Ipomoea* hexaploids by hybridization of diploid *I. leucantha* and tetraploid *I. littoralis* (Nishiyami, Miyazaki and Sakamoto, 1975.). The Spanish introduced sweet potato in the

sixteenth century into the Philippines, whence it spread to other islands and the east Asian mainland. Portuguese seafarers introduced the crop into Europe, Africa and India. Today it is cultivated in 117 countries in all tropical and subtropical regions of the world. Asia is the world's largest sweet potato producing region, with about 107 million tonne of annual production, followed by Africa and the Americas, with approximately 15 and 3 million tonne, respectively. The top 12 producing countries are China (80 percent), Nigeria (2.8 percent), Uganda (2.2 percent), Indonesia (1.5 percent), Viet Nam (1.2 percent), United Republic of Tanzania (0.9 percent), Japan (0.8 percent), India (0.8 percent), Burundi (0.7 percent), Kenya (0.6 percent), Rwanda (0.6 percent) and United States of America (0.6 percent). Further important sweet potato producing countries are Angola, Argentina, Bangladesh, Brazil, Cuba, Egypt, Ethiopia, Haiti, Korea (Democratic Republic of), Madagascar, Peru, the Philippines and Papua New Guinea, with annual production between 0.3 and 0.5 million tonne (FAO, 2006). Nearly half of the sweet potato produced in Asia is used for animal feed, with the remainder primarily used for human consumption, either as fresh or processed products. In Africa, the crop is cultivated almost exclusively for fresh consumption.

Sweet potato is a perennial vine, propagated by cuttings, and usually cultivated as an annual crop. The planting distances in fields vary. In Africa, planting distances are usually 1 m between rows and 30 cm within rows. In China, recommended planting distances are 75 cm between rows and 20 cm within rows. The crop duration is very short (4 to 6 months) and the crop is even cultivated in northern China. It produces more edible energy per hectare per day than wheat, rice or cassava, and is well

adapted to salinity, drought and marginal soil conditions (Woolfe, 1992).

The crop has recently received more interest due to the very high levels of pro-vitamin A (concentrations of up to 700 ppm DM) in OFSPs, and hence as a vehicle to reduce vitamin A deficiency problems in the world (Huang, Tanudjaja and Lum, 1999; Low, 2007). We observed up to 1 200 ppm β -carotene on a DM basis in clones with variety potential in our breeding population 'Jewel II' (this corresponds to 30 mg β -carotene in 100 g fresh sweet potato storage roots. A preschooler needs 4.8 mg β -carotene per day, and it merits discussion as to what extent OFSP should be recommended as baby and weaning food. Moreover, storage roots provide medium levels of iron and zinc (Woolfe, 1992). Recent finding of about 50 ppm DM iron and 40 ppm DM zinc in deep orange fleshed sweet potato storage roots (Burgos and zum Felde, pers. comm.) merits further investigation.

The stems and leaves can have spinach-like taste and some varieties are used in China specifically as a green vegetable. Stems and leaves have on DM basis about four times more protein, iron and zinc than storage roots. It appears that stems and leaves must be cooked to reach an acceptable iron bioavailability, but investigations into iron bioavailability of sweet potato tops is very limited.

There is new demand for purple-fleshed sweet potato due to the health-promoting effects of anti-oxidant anthocyanin substances, and cell lines for a potentially ongoing production for the food industry have been established (Konczak, 2006). However, much more important appears to be the demand for non-sweet sweet potatoes, but few genotypes are non-sweet (Kays, 2006). There is a very large genetic

variation for DM, starch and sugars in sweet potato, and a strong positive correlation has been observed for DM and starch, whereas a strong negative correlation was found between sugars and DM and starch (Grüneberg *et al.*, 2009). This is nearly ideal for the breeding target of a non-sweet high-DM sweet potato type, and we think that the development of non-sweet sweet potatoes should not be too difficult.

Breeding objectives

FPB started very late for sweet potato. One of the first breeding programmes was established at Louisiana State University in the 1920s. Today there are several strong national breeding programmes (e.g. China, Japan, South Africa, Uganda, United States of America and Uruguay) and one international breeding programme, at CIP (Peru). Four major breeding objectives can be clustered: (i) breeding of OFSP for consumption of storage roots and leaves; (ii) breeding for high DM and extractable starch; (iii) breeding for biofuel production, which has started in China (Dai Fu Ma, pers. comm.); and (iv) breeding of purple-fleshed sweet potatoes for consumption. In breeding for consumption, it has to be considered that people in different regions have very different taste preferences; the extremes are low DM content, moist mouth feel, very sweet taste and deep orange flesh colour, versus high DM, bland, dry mouth feel, low sweet taste and white, yellow or orange flesh colour. In breeding for human consumption, focus is more on high DM OFSP varieties with elevated iron and zinc concentration and a dry and less-sweet mouth taste. This breeding is hampered by a strong negative genetic correlation between storage root DM and storage root pro-vitamin A, iron and zinc contents. The breeding for human consumption includes

the use of the crop as animal feed and fodder. The breeding for high DM and extractable starch is relatively easy: the target is a high starch yield per hectare. However, currently, in many regions of the world the price of sweet potato starch currently cannot compete with the price of cassava starch. Only in large regions where the growing period is too short for cassava within the cropping system (e.g. China) is there an economic demand for sweet potato varieties for starch production. Breeding for biofuel production is in its initial stages, and so far variety recommendations for this purpose are made on the basis of screening existing successful varieties. The breeding of purple-fleshed sweet potatoes as a separate breeding programme is a relatively new trend, and so far only carried out on a small scale in Japan, Indonesia and Peru. Future targets are the non-sweet sweet potato, and quick cooking features (cv. Quick Sweet) (Katayama *et al.*, 2006), as well as suitability for processing into chips, puree, juice, weaning and baby food, and bread on the basis of a wheat-sweet potato flour mixture (Woolfe, 1992); these trends appear nearly exclusively in east Asia, and for recent developments the reader should consult proceedings, such as Liu (2008).

Major constraints on high yields are pests and diseases, especially Sweet potato chlorotic stunt virus (SPCSV) and the sweet potato weevils. The prevailing diseases and insects affecting sweet potato vary from region to region. There are about 35 bacterial and fungal diseases, more than 20 viruses or virus-like agents, 20 nematodes and 20 insect species known to affect sweet potato (Martin and Jones, 1986).

Currently there are only four important pest and diseases: SPVD, *Alternaria*, sweet potato weevils and the root-knot nematode. The most important virus is whitefly-

transmitted SPCSV, which often occurs in co-infection with Sweet potato feathery mottle virus (SPFMV – aphid-transmitted). Clear synergistic disease effects are seen with SPFMV and SPCSV (the so-called SPVD virus complex). Generally, all varieties need a certain degree of tolerance to SPVD, and there is genetic variation for SPVD (Mwanga, Yencho and Moyer, 2002). Very high tolerance or resistance is needed in eastern Africa. Currently, it is assumed that SPFMV and all other sweet potato viruses (except SPCSV) are not important, because sweet potato has an effective virus defence system, which is broken by SPCSV (I. Barker, pers. comm.).

The major fungal disease in subtropical America is Fusarium wilt (*Fusarium oxysporum* f.sp. *batatas*) and in the African highlands the main problem is Alternaria storage root, leaf spot and stem blight (*Alternaria* spp.). Although there are many bacterial and fungal diseases with a wide distribution, high levels of tolerance or resistance are frequently found. This is also true for resistance to nematodes.

There has been recurrent success in breeding for root-knot resistance against new races of *Meloidogyne* spp. (Martin and Jones, 1986). However, in regions with a pronounced dry season, the greatest constraints are sweet potato weevils (*Cylas formicarius elegantulus* in all parts of the tropics, *C. puncticollis* and *C. brunneus* in Africa, and *Euscepes postfasciatus* in the West Indies). It has been an objective to find weevil resistance for more than 50 years, but differences in weevil attack probably depends on preference factors of the weevil. It is believed that dense storage roots developed deep below the soil surface are less susceptible than less dense, moist-fleshed storage roots. No effective weevil resistance has been found so far. For

this reason, a transgenic approach using *Bt* genes has received attention. Recent findings of compounds in the latex of the storage root skin and the effect of these on weevils might of interest for breeding (P.C. Stevenson, H. Muyinza, D. Hall and R. Mwanga, unpubl.).

Breeding methods

True seed set occurs easily in nature by cross pollination (by insects, mainly bees), and for breeding purposes the flower architecture of sweet potato allows easy emasculation and controlled hand pollination. A skilled technician can make 200 crossings per day, with a success rate of 25 percent. From each successful cross, two or three true seeds are obtained. Not all sweet potato parents flower readily, but flowering can be easily induced by grafting on *Ipomoea nil* ($2n = 30$ chromosomes). It should be noted that frequencies of successful crosses differ tremendously between parental combinations, and about one-third of all parental combinations are incompatible, with no seed formation. The sweet potato seed has a hard coat and needs to be scarified with concentrated sulphuric acid to obtain even and rapid germination. In a well managed breeding nursery, after 3 months it is possible to obtain 40 to 60 cuttings from a true seed plant if the plant is grown in the field, and 20 to 30 cuttings if the plant is grown in a pot in a greenhouse. The extreme genetic make up of the crop (hexaploid, highly heterozygous, open-pollinated by insects with true seed set occurring easily), the short crop duration (4–5 months), and the rapid propagation (40 to 60 cuttings from one plant) permits the design of a very efficient and rapid breeding system.

The recombination of parents is still usually carried out in polycross nurseries

by open pollination. Polycrosses have been considered as very efficient in sweet potato breeding (Martin and Jones, 1986). However, theoretically controlled crosses must be more efficient, provided that high selection intensities can be reached, which depends on technical skills and costs. Only a few breeding programmes are making (at least to any major extent) controlled crosses (e.g. in China, Mozambique, Peru and Uganda). The numbers of recombined parents vary between 20 and 120, and the number of genotypes raised per population (true-seed plants) varies between 5 000 and 30 000. Selection of parents is almost exclusively carried out on the parental performance *per se*. In China, Uganda and at CIP in Peru, the information from progeny test crosses is used to repeat good cross combinations on a larger scale (2 000 to 3 000 genotypes per cross). In recent years, CIP has established two genetically divergent populations to test heterosis and general combining ability in applied breeding material. There are plans to change from a selection of parents by parental performance *per se* to a reciprocal recurrent selection scheme based on general combining ability. Selection of genotypes for variety development is usually carried out as described in the section of the general breeding scheme for clonally-propagated crops. Starting with recombining parents, it takes on average 7 to 8 years until variety release. At CIP, Peru, an accelerated breeding scheme is used in which temporal variation of test environments are replaced by spatial variation of test environments. This accelerated breeding scheme takes on average 3 to 4 years until variety release. It appears that there are funding opportunities to implement this breeding scheme in Africa, particularly in Ghana, Uganda and Mozambique.

13.12 CASSAVA

Breeding cassava has been reviewed by Byrne (1984), Bonierbale *et al.* (1994) and Ceballos *et al.* (2004). Cassava (*Manihot esculenta*, Euphorbiaceae, diploid with 36 chromosomes) originated in South America. The crop is also known as *manioc* and *yucca*. Wild *Manihot* species—weedy sub-shrubs, shrubs and trees—are principally found in dry regions of Mesoamerica and South America. The highest density of diversity is found in west-central Brazil. Many wild *Manihot* species show considerable tuber production and it is assumed that *M. esculenta* was selected from one or several of these wild species in the northern part of South America or in west-central Brazil. The crop was disseminated by tribal migrations and its variability increased by selection for agronomically preferred types and further hybridization with wild species. Cassava was introduced in the fifteenth century into West Africa by the Portuguese from Brazil, and from there it spread to eastern Africa, Madagascar and southern India. Moreover, it was introduced in the sixteenth century into the Philippines by Spanish traders from Mesoamerica. Today the crop is cultivated worldwide in lowland tropics. World production of cassava root was estimated to be about 226 million tonnes in 2006, with most production in Africa, where 122 million tonnes were grown, while 67 million tonnes were grown in Asia and 37 million tonnes in Latin America and the Caribbean (FAO, 2006). The top ten cassava producing countries are: Nigeria (18 percent of world production), Brazil (12 percent), Thailand (10 percent), Indonesia (9 percent), Democratic Republic of the Congo (8 percent), Ghana (5 percent), United Republic of Tanzania (4 percent), India (4 percent), Mozambique (3 percent), and Angola (3 percent).

Cassava adapts to a wide range of ecological conditions and is known for its tolerance of low soil fertility, drought and pests. The growing period is long, between 7 and 18 months. The yields are very high (about 30 to 40 t/ha under commercial practice). However, the protein content of cassava is low (<3 percent DM), which makes the crop ideal for starch production. Cassava is often grown in low input production systems, particularly when it is grown as a food crop. Planting material is easily obtained from plant stems available from the farmers' own or neighbouring fields. About 70 percent of cassava is grown by small-scale producers for direct human consumption. The crop tolerates more drought, lower soil levels of nitrogen, potassium and phosphorus, lower pH and higher aluminium levels than most other crops. Under these conditions, yields are about 7–10 t/ha. Cassava is often found in mixed stands, together with a variety of other food or cash crops. Estimates indicate that at least one-third of the cassava grown worldwide is intercropped (Cock, 1985).

Breeding objectives

FPB started in isolated programmes in the early 1900s when cultivation was extended by several colonial governments as a safeguard against famine, and breeding new clones with resistance against cassava mosaic disease (CMD) was required. Cassava breeding programmes started in Brazil (in the 1930s), India (in the 1940s), Indonesia (in the 1950s) and at two international institutions: CIAT, Colombia, (in the 1970s) and IITA, Nigeria, (in the 1970s). These institutions have developed a very successful cassava breeding network.

In cassava breeding, three diseases have been the highest priority for decades: (i) Cassava mosaic disease (CMD), which is

a whitefly-transmitted virus widespread in Africa and India; (ii) Cassava brown streak disease (CBSD); and (iii) Cassava bacterial blight (CBB), caused by *Xanthomonas campestris* pv. *manihotis*, which can have devastating effects on yield in Africa. Of regional importance in Latin America and the Caribbean is Frogskin disease, suspected to be caused by a virus. Aside from these, cassava is much less affected by disease than other tropical crops, the only other two of importance being Cassava anthracnose disease (*Colletotrichum manihotis*) and root rots (*Phytophthora drechsleri* and *Rhizoctonia* spp.) (CIAT 2001; Hillocks and Wydra, 2002).

The major pests of cassava are nematodes (*Meloidogyne* spp.), whiteflies as a vector of CMD, Cassava green mites (*Mononychellus* spp. and *Tetranychus* spp.), cassava mealybug (*Phenacoccus* spp.), and the grasshopper (*Zonocerus elegans*). Pests and diseases, together with poor cultural practices, combine to cause yield losses as high as 50 percent. In the late 1980s, a new strain of CMD occurred in Uganda that made the virus more harmful. This mutated virus has been spreading and is now found throughout Uganda, Burundi, Cameroon, the Democratic Republic of Congo and Rwanda (Thresh and Cooter, 2005). Next in importance in breeding are more short and thick storage roots with high starch content. This is important for mechanical harvesting, but makes also manual harvesting easier. It is desirable for the roots to be as far as possible horizontal in the soil and near to the soil surface. Breeding selects for plants with lower height and higher harvest index. In cassava breeding for human consumption, the focus is on yield and quality such as low fibre, low levels of cyanogenic glucosides, high protein, elevated pro-vitamin A, iron and zinc concentration in the storage roots, reduced

post-harvest physiological deterioration and regional preferences for the peel of the roots (Ceballos *et al.*, 2004). Cassava varieties are often categorized as either 'sweet' (actually 'not bitter') or 'bitter', signifying the absence or presence of toxic levels of cyanogenic glucosides. The so-called 'sweet' cultivars can produce as little as 20 mg/kg cyanide in fresh roots, while 'bitter' ones may produce more than 50 times as much. Additionally, an important breeding objective is to develop more clones with high adaptation to drought-prone environments. The genetic variation in cassava for pro-vitamin A concentrations is small. However, breeding for yellow cassava genotypes with a pro-vitamin A concentration of 15 ppm appears to be possible. Additionally, a transgenic approach is used to introduce the β -carotene pathway into cassava (J. Tohme, pers. comm.). Breeding for commercial production also selects for plants with shorter height and higher harvest index – giving more stability and resistance against storms – and extensive branch formation, quickly forming a full canopy of leaves not too close to the soil (Byrne, 1984).

Breeding methods

Cassava is a monoecious, highly heterozygous plant. All 36 chromosomes show regular bivalent pairing at meiosis. However, in both cassava and *Manihot glaziovii* (sect. *Arboreae*) there is evidence of polyploidy from studies of pachytene karyology. There are three nucleolar chromosomes, which is high for true diploids, and duplication for some of the chromosomes. This indicates that *Manihot* species are probably segmental allotetraploids derived from crossing between two taxa whose haploid complements had six chromosomes in common but differed in the other three (Nasser, 2000). Cassava shows self-fertility with strong inbreeding

depression and wide segregation in cross progenies. Time of flowering depends on the genotype. There are types in which flowering starts about two months after planting, as well as types that do not flower until after 24 months or more. This makes planned recombination difficult. Earlier and more abundant flowering is obtained by foliar application of indole acetic acid (IAA) and naphthalene acetic acid (NAA). The female flowers are large, nearly always located at the base of the inflorescence, and open first. The female flowers normally open 10–14 days before the males on the same branch, but self-fertilization can occur because male and female flowers on different plants of the same genotype can open simultaneously.

The proportions of self- and cross-pollinated seed produced depends on genotype, planting design and the type of pollinating insects present (5 percent self-pollination occurs naturally). Both the stigma and the pollen are sticky and pollination is easily carried out by honey bees. In the Northern Hemisphere, cassava usually flowers from July to January, with a peak between September and November. In the Southern Hemisphere, it usually flowers from January to July, with a peak between March and May. Tall plants with less branching are less floriferous than highly branched, low growing ones. To make a controlled cross between two parents, unopened flowers are first enclosed in muslin bags and the chosen pollen applied to the stigmas as soon as the female flowers open. The muslin bags are then replaced with netting bags to catch the seed when the ripe fruits dehisce explosively. The fertility of clones is variable and can be very low; an average of one or two seeds per fruit is common in controlled pollination. Seed matures 70 to 90 days after pollination. The fruits are collected when the coat begins to

shrive and are sun dried until they shatter, releasing hybrid seeds that are ready for germination. Cassava seeds have a very short dormant period and germinate quickly. No scarification is necessary. Few seeds germinate unless the mean temperature exceeds 24°C, with a temperature exceeding 30°C for at least part of the day; the best rates occur at 30–35°C. A dry heat treatment of 14 days at 60°C is also beneficial for newly harvested seeds. If temperatures permit and irrigation is available, the easiest method is to sow the seeds direct into the soil. This is successful at IITA because temperatures from January to March range from 30° to 35°C. At CIAT, seeds are frequently planted in a screen house and the emerging seedlings held until they reach 20–25 cm before being transplanted to well prepared soil with good moisture conditions.

Since many national programmes do not have a continuous cassava crossing programme, they rely on distribution of pre-selected clones from the two international institutions, CIAT and IITA. The improved germplasm generated is distributed either in the form of elite genotypes transferred *in vitro*, or as populations of recombinant seeds (full-sibs or half-sibs). Cassava breeding operates with larger populations than potato or sweet potato.

In West Africa, up to 100 000 true seed plants are raised from field-sown seed, which are screened in a first selection step for resistances to CMD and CBB. At harvest, selection is for compact roots with short necks, stems branching at about 100 cm, with low HCN in the leaves. In the second selection step, about 3 000 clones are grown in small, non-replicated plots. Further selection is made for disease resistances, yield potential and root DM content, and the HCN in the roots is assayed enzymatically. For the third selection step,

ca. 100 clones are tested in replicated trials at three locations, and consumer acceptance is assessed. Final selections are multiplied and enter dissemination in year 6.

In eastern and southern Africa, 10 000 to 50 000 true-seed plants are raised for the first selection step and screened for resistance to major diseases and pests at 1, 3, 6 and 9 months after sowing, namely East African cassava mosaic disease (EACMD), African cassava mosaic disease (ACMD), Cassava brown streak disease (CBSD) and CBB. In a second selection step, 2 000 clones are planted in single-row plots (3 to 5 plants) at 1×1 m spacing. The observations made in the first year are repeated again at 1, 3, 6 and 9 months after planting. Each clone is scored for yield, and agronomic characteristics assessed, such as branching height and angles, canopy and number of stems per plant. In a third selection step, 20 to 50 clones are grown in preliminary yield trials in single rows with ten plants per clone and three replications at one to three locations. In year 6, the final selections are taken on-farm and into national variety release trails.

In the Americas and Asia, cassava improvement is closely linked with the institutions Embrapa (Brazil), FCRI Rayong (Thailand) and CIAT (Colombia). In contrast with Africa, there are no extremely devastating diseases. CIAT established 50 000 seedling selections for particular climatic zones. Up to 20 parents from each gene pool are disseminated for evaluations to national centres in similar edapho-climatic zones. From this programme a very broad range of improved diversity has been developed and distributed worldwide.

Generally, MVs in Asia can be traced back to 100 crosses between Asian and American parents (Kawano, 2003). Recent findings show that the general combining ability for cassava fresh root yields are clearly larger

than the specific combining ability across contrasting environments (Ceballos *et al.*, 2004). This is a clear indication that heterotic gene pools in cassava can be formed and exploited by improving two gene pools with a reciprocal recurrent selection scheme.

13.13 BANANA OR PLANTAIN

Breeding bananas and plantains has been reviewed by Rowe (1984), and Jain and Swennen (2001) have edited recent proceedings on banana improvement, with a main emphasis on biotechnology. Banana and plantain (*Musa* × *paradisiaca*, Musaceae, usually triploid with 33 chromosomes) originated in Southeast Asia. The term plantain is used for those bananas that are palatable only when cooked. The crop was introduced into Africa about 3 000 BPE. Introduction into the Americas came after 1 500 AD. Today the crop is cultivated worldwide in the tropics. Bananas and plantains evolved from two diploid wild species, *Musa acuminata* (AA) and *M. balbisiana* (BB) in the Eumusa series ($x = 11$) of the genus *Musa*. An exception is the small group of 'Fehi' bananas in the Australimus series ($x = 10$) of *Musa*. All export fruit bananas are triploids (AAA) and originated from *M. acuminata*. All plantains and several locally preferred fruit bananas are hybrids between *M. acuminata* (AA) and *M. balbisiana* (BB). The higher dry matter (about 5–8 percent) and higher starch content of plantains compared to pure *M. acuminata* cultivars is attributed to the BB genome. The AAB cultivars have long curved fruits and appear like an oversized export banana. They are important food crops in south India, eastern and central Africa and tropical America. The ABB cultivars have thick straight fruits, which are much shorter than the AAB types

(Simmonds, 1976; Ortiz, 1995). They are a staple in Samoa, the Philippines, south India and the West Indies. Around 87 percent of all bananas and plantains grown worldwide are produced by small-scale farmers for home consumption or for sale in local markets. About two-thirds of world production is dessert bananas and one-third plantains. The fruit export market comprises only one-sixth of total world production. The banana is the number one fruit crop in the world, with about 70.5 million tonne produced annually. The top ten producing countries are India (24 percent), Ecuador (9 percent), Brazil (9 percent), The Philippines (8 percent), China (8 percent), Indonesia (5 percent), Costa Rica (3 percent), Mexico (2 percent), Thailand (2 percent) and Colombia (2 percent). Plantains are grown as a staple food in 52 countries worldwide with a total production of 34 million tonne. The top ten plantain producing countries are Uganda (30 percent), Colombia (9 percent), Rwanda (8 percent), Ghana (7 percent), Nigeria (6 percent), Peru (5 percent), Cote d'Ivoire (4 percent), Congo (4 percent) and Kenya (3 percent) (FAO, 2006).

Bananas and plantains are one of the very few crops in which breeders are still trying to find an appropriate conventional breeding method to develop new MVs. Nearly all cultivars are FVs and have been selected from genetic variation developed by natural evolution. In cases of crop failure due to new pathogens and diseases, FPB still focuses on identifying alternative cultivars within existing genetic variation (collections and large screening programmes). Hence, an important source for identifying 'new' cultivars are germplasm collections held in trust in genebanks, such as the International Musa Germplasm Collection in Leuven, Belgium. Spontaneous mutants in *Musa* have played a very important role in banana and

plantain breeding, including the replacement of the export banana cultivar 'Gros Michel' (susceptible to Panama disease or Fusarium wilt (*Fusarium oxysporum* sp. *cubense*) by 'Cavendish' banana cultivars, which are resistant to most fusarium wilt pathogens, and the replacement of the plantain cultivar 'Horn plantain' (AAB) (susceptible to Black sigatoka (*Mycosphaerella fijiensis*)) by the 'Laknau' cultivar (AAB), which is tolerant to Black sigatoka and closely resembles the Horn plantain (Stover, 1972). However, the cooking qualities of Laknau are inferior to Horn plantain. Owing to the low level of occurrence of spontaneous mutations, mutagenic agents and mutation breeding have often been used to generate new genetic variation in bananas and plantains, followed by screening programmes for plants with resistance or tolerance to pest and diseases, coupled with desirable agronomic qualities (e.g. tolerance to Panama disease; tolerance to the toxin of *Mycosphaerella fijiensis*; short; larger fruit size; and earliness). The FPB programmes for bananas and plantains started in the early 1900s, to develop new AAA cultivars for the export market, with resistance against Panama disease or Fusarium wilt (*Fusarium oxysporum* f.sp. *cubense*). Despite continued breeding efforts, no new banana and plantain cultivar acceptable by farmers and consumers was bred until the 1980s (Roux, 2001). Nevertheless, by the end of the twentieth century, efforts to improve *Musa* started to focus on the use of diploid and tetraploid gene pools to develop triploid and tetraploid bananas and plantains. To date, the first improved cultivars (AAA, AAAA, AAB, AAAB and AABB), developed at *Fundación Hondureña de Investigación Agrícola* (FHIA) in Honduras through the International Musa Testing Program (IMTP), have been

widely distributed. However, for several of these FHIA cultivars, taste and cooking qualities are still problematic (Roux, pers. comm.). Further breeding programmes have been set up at the *Empresa Brasileira de Pesquisa Agropecuária* (Embrapa) in Brazil, the *Instituto de Investigaciones en Viandas Tropicales* (INIVIT) in Cuba, the *Centre Africain de Recherches sur Bananiers et Plantains* (CARBAP) in Cameroon, the International Institute of Tropical Agriculture (IITA) in Nigeria, and the National Research Centre on Banana (NRCB) in India.

Breeding objectives

In breeding, resistance against Panama (Fusarium wilt) and sigatoka diseases are in the foreground. In the first half of the twentieth century, Panama disease destroyed approximately 40 000 ha of bananas in Central and South America. Fortunately, resistant Cavendish cultivars could substitute for the predominantly grown Gros Michel variety. However, Cavendish cultivars are not resistant to all fusarium wilt pathogens (i.e. race 4). It should be noted that Panama disease cannot be controlled chemically, so that use of resistant varieties is the only way to maintain production in regions with challenge from this disease. The leaf spot diseases caused by *Mycosphaerella musicola* (Yellow sigatoka) and *M. fijiensis* (Black sigatoka) are costly pathogens and must be regularly controlled by fungicides. Cultivars with an AAA genome are very susceptible to both sigatoka diseases. The Horn plantain is resistant to Yellow sigatoka, but susceptible to Black sigatoka. The latter disease threatens continued cultivation of the plantain food crop. Triploid cooking bananas of the ABB type, such as 'Chato', 'Pelipita' and 'Saba', are highly tolerant to the Black sigatoka pathogen. However,

Chato is susceptible to bacterial wilt or Moko disease caused by *Pseudomonas solanacearum* and to race 2 of *Fusarium oxysporum* f. sp. *cubense*, while Pelipita does not meet flavour and fruit-shape preferences, so that currently only Saba remains as a possible substitute for the Horn plantain. Moreover, nematodes, mainly the burrowing nematode (*Radopholus similis*), are a major constraint to bananas in monoculture, and outside of the Americas the Bunchy top virus is widely distributed, which is transmitted by the banana aphid (*Pentalonia nigronervosa*). Many diploid accessions of *M. acuminata* subsp. *malaccensis* and *M. a.* subsp. *burmannica* are resistant to races 1, 2 and 4 of Panama disease. Sources of resistance to Yellow sigatoka are available in several subspecies of *M. acuminata*, while *M. a.* subsp. *burmannica* is highly tolerant to the Black sigatoka fungus. The tolerance in *M. acuminata* accessions to sigatoka diseases is apparently controlled by several dominant genes. Resistance to the burrowing nematode has been found in the 'Pisang Jari Buaya' group of diploid accessions. The resistance is controlled by one or very few dominant genes and has been incorporated into diploid and polyploid progenies. Today, several FHIA varieties are resistant to burrowing nematodes (Kalorizou, Gowen and Wheeler, 2007).

Among agronomic qualities, dwarfness is most important in bananas and plantains, because they are often grown in areas with periodic strong winds. Dwarf and semi-dwarf mutants have been found in many diploid and triploid bananas and plantains. Examples are 'Highgate' (a dwarf mutant of Gros Michel) and the Cavendish cultivar 'Grand Nain'. In dwarf diploids, the dwarfness character is controlled by a single dominant gene. After this in importance are fruit characteristics and

tillering capacity (Ferwerda and Wit, 1969; Rowe and Richardson, 1975; Persley and De Langhe, 1987).

Breeding methods

Triploid bananas and plantains are vegetatively parthenocarpic, i.e. no pollination is necessary for fruit development. In diploids, pollination often results in seeded fruits. Diploids are not suitable as varieties since fruit size and plant vigour are low. However, diploids are the basis for crop improvement. In the initial stages of breeding efforts, a few seeds per bunch in some triploid varieties were used when these had been pollinated by diploid genotypes. The reason for this seed production and genetic variation is the formation of unreduced triploid gametes in some triploid female parents after pollination within diploid male parents, which produces reduced haploid gametes. The progenies of these crosses are tetraploid. This method was used to generate genetic variation with the female banana parent Gros Michel and the female plantain parent Laknau (AAB), which closely resembles the Horn plantain. Tetraploid hybrids (AAAA) from crosses with Gros Michel were resistant to Panama disease and closely approached commercial acceptability, but the inferior agronomic characteristics of the diploid parents were also present in the hybrids. Triploid hybrids derived from crosses between these tetraploid hybrids and diploid genotypes were useless. Unfortunately, the cooking qualities of hybrids derived from Laknau were also inferior to those of the Horn plantain. No seeds have been produced from Cavendish clones and no other suitable triploid parents—except Gros Michel and Laknau—for seed production by unreduced gametes have been found. This breeding method has not succeeded in creating acceptable new varieties. However,

the major finding of this work was that it is necessary to improve the diploid male parent gene pool to increase the chances of developing either new tetraploid or new triploid varieties.

Today, banana and plantain breeding aims at producing tetraploid and triploid varieties on the basis of diploid accessions resistant to various diseases, and the continuous improvement of this diploid gene pool for agronomic qualities (i.e. plant height, fruit characteristics and tillering capacity) as well as high pollen production. Crossings within the diploid gene pool are complex: the diploid 'SH-2095', which was later successfully used in tetraploid variety development, was derived from a four-way cross of three diploid cultivars and one wild accession (('Sinwobogi' × 'Tjau Lagada') × ('Guyod' × a wild *Musa acuminata* subsp. *malaccensis*)). Nevertheless, the genetic basis of diploid pollen parents with improved agronomic performance is considerably wider than in the past. The currently best diploids are continually crossed on triploid Highgate and Laknau, which produces unreduced triploid gametes, as well as on seed-fertile tetraploids with good agronomic performance. The first results in new potentially tetraploid varieties and the later in new potentially triploid varieties. The advantage of triploids in variety development is that they are female-sterile due to the uneven number of chromosome sets. In contrast, the even number of the chromosome set in tetraploids requires an additional selection step for female sterility in variety development. Several improved FHIA cultivars (AAA, AAAA, AAB, AAAB and AABB) have been developed by this breeding method, and farmers participate in the final breeding stages in acceptability studies of these tetraploid and triploid varieties (i.e. PVS) (Ssemwanga,

Thompson and Aked, 2000; Ludger, 2005; Kalorizou, Gowen and Wheeler, 2007). However, to our knowledge, no PPB has been applied in early breeding stages. Most likely the reason for this is that almost no diploid clone in its performance *per se* would achieve acceptability by farmers. Nevertheless, the future of banana and plantain breeding, as in other clonally propagated crops, should be seen in testing the combining ability between two gene pools and in the improvement of two gene pools on the basis of the general combining ability and reciprocal recurrent selection. In banana and plantain breeding, such a breeding system can be established by a seed-fertile diploid gene pool with high pollen production and a seed-fertile tetraploid gene pool, which is used as the male parent. In such a breeding programme, PPB could easily be incorporated. However, the important information provided by the farmers would not be seen in the evaluation of clone performance *per se* in the diploid and tetraploid gene pool, but in the numbers of acceptable clones per cross combination and family between genotypes of the diploid and tetraploid gene pool, as described above in the section on selection of parents and cross prediction.

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CHAPTER 14

Breeding for quantitative variables. Part 1: Farmers' and scientists' knowledge and practice in variety choice and plant selection

Daniela Soleri and David A. Cleveland



14.1 INTRODUCTION

This chapter focuses on the knowledge and goals for selection of Third World farmers in comparison with those of formal plant breeders. By Third World farmers (hereafter simply ‘farmers’) we mean those in the relatively marginal (high stress, high spatial and temporal variability) growing environments of small-scale, traditionally-based agricultural systems (hereafter simply ‘small-scale’ or ‘Third World’ agriculture).

The assumption of conventional economic development has for decades been that these farmers would soon be absorbed into the industrial sector, and food production would shift to large-scale, industrial farms, and this scenario is still seen as desirable by many (e.g. Conway, 2003). There is, however, evidence that this small-scale Third World (SSTW) agriculture remains necessary for feeding a significant proportion of the world population, and will probably be necessary in the future, even with production increases in large-scale, industrial agriculture (Hazell *et al.*, 2007). More than 2 billion people live on almost 500 million small-scale farms (<2 ha) in the Third World, including half of the world’s undernourished people and the majority of people living in absolute poverty (Nagayets, 2005). Economic re-structuring beginning in the 1980s removed government support for SSTW agriculture and led to migration from rural to urban areas, creating a crisis there (Hazell *et al.*, 2007; Narayanan and Gulati, 2002; Wise, 2007). In addition to irreplaceable food production, SSTW agriculture has other benefits: it operates in many of the world’s centres of crop genetic diversity, where farmers conserve diversity in the form of crop genetic resources *in situ*, along with rich cultural and linguistic traditions (FAO, 1996; Harlan, 1992). Plant or crop genetic resources comprise wild and weedy relatives of crops in addition

to farmers’ varieties (FVs), which include landraces, traditional (folk) varieties selected by farmers, modern varieties (MVs) adapted to farmers’ environments by farmer and natural selection, and progeny from crosses between landraces and MVs (sometimes referred to as creolized or degenerated MVs) (Berg, 2009; Cleveland, Soleri and Smith, 1994; FAO, 1996; Zeven, 1998). Sustaining and increasing crop production is essential for the survival of SSTW agriculture, and, in this, seed saving and plant breeding have critical roles to play

In this chapter we review theory and data on selection by farmers, and compare it with selection by formal, scientific plant breeders (hereafter simply ‘plant breeders’ or ‘breeders’). Because selection by farmers and formal plant breeders is based on the same basic biological principles, their understanding and practice of selection may be similar. However, there are differences between farmers and breeders in the genotypes and environments they work with, including the types of agricultural systems for which they are selecting, as well as differences in their experiences, technologies and goals for selection. Similarities and differences in selection among farmers and among formal plant breeders also exist, for the same reasons. Our goal in this chapter is to review what we know about these similarities and differences, and why understanding them is important for collaboration between farmers and breeders to improve selection for varieties that could help SSTW farmers survive and prosper in the future.

We believe that respect for farmers and their knowledge is essential for achieving the maximum benefits from collaborative plant breeding. The greatest single mistake plant breeders and other outside scientists can make is to assume they understand local agricultural systems. Even if their hypothe-

ses are accepted through local research, new details and perspectives are sure to arise, and it is only by having an open minded, respectful attitude that outsiders can hope to learn and reap the benefits of collaboration with local farmers. Such an attitude facilitates new insights and understandings that can improve the accuracy and relevancy of the scientific work. If plant breeders think of their interactions with farmers as tests of how complete or accurate farmers' knowledge is, breeders will lose a critical opportunity for supporting collaboration, respect and collegiality, and for improving the quality of their own work. Thus, at least initially, experiments and discussions with farmers should be seen as opportunities to learn, not to teach.

14.1.1 Choice as distinct from selection

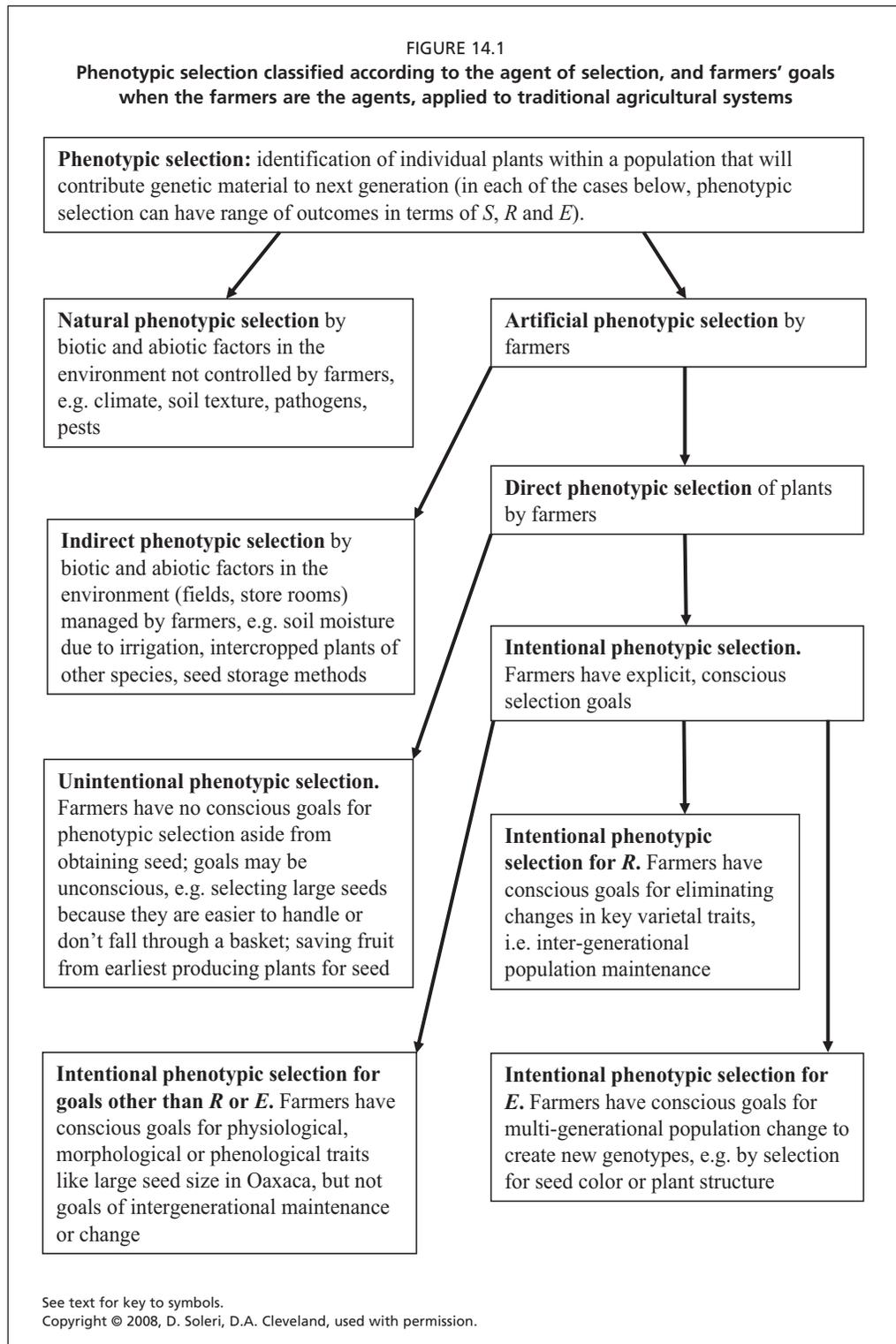
It is important to differentiate between *choice* of populations or varieties that does not change the genetic make-up of these units, and the *selection* of plants from within populations or varieties, with the potential to change the genetic make-up of these units, which may eventually result in new varieties (Cleveland, Soleri and Smith, 2000). Farmer criteria for both choice and selection include agronomic, economic, culinary and aesthetic characteristics, as well as minimizing perceived risk. While the distinction is commonly made in some participatory plant breeding literature (e.g. Witcombe *et al.*, 1996), the terms 'choice' and 'selection' are often not explicitly defined, and in some writing may be used interchangeably. Obviously, distinguishing between these is partly a function of scale, as is most clearly seen in the case of vegetatively propagated crops, in which a single clone may be chosen to establish a new variety (e.g. with cassava; Pujol, David and McKey, 2005). It also depends

on definitions: a farmer's variety of a self-pollinated crop (e.g. of barley or rice) may be composed of diverse genotypes that, from a plant breeder's perspective, may be different varieties. Therefore discriminating among these genotypes would be selection from the perspective of farmers as it can change the genetic make up of their variety, but would be choice from the perspective of plant breeders as it would not change the genetic make-up of varieties as they define them. At a more fundamental level, farmers' choice of populations and varieties determines the diversity available for hybridization and subsequent selection of plants. For all of these reasons, we can say that selection and choice together determine the degree to which varieties stay the same, change between generations, or evolve over generations.

Farmers and plant breeders make choices between varieties and populations, especially in the initial stages of the selection process when choosing germplasm for making crosses (for plant breeders), and in the final stages when choosing among populations or varieties generated from those crosses for further testing (Hallauer and Miranda, 1988: 159), or for planting (farmers) or release (plant breeders). Farmers' choices of varieties or populations when saving seed for planting, in seed procurement and in allocating different varieties to different growing environments also affects the genetic diversity of their crop repertoires, and establishes the diversity on which future selection will be based. (For simplicity, in the discussion of choice we will use the term 'variety' to refer to both populations and varieties.)

14.1.2 A taxonomy of farmer selection

A taxonomy of selection and its biological effects can help to clarify the differences



and similarities between plant breeders and farmers. Selection can be categorized according to the agent carrying out phenotypic selection, and the intention of the agent when it is a human (Figure 14.1). While all types of selection function in both farmer and professional breeding, professional plant breeders see intentional phenotypic selection for micro-evolution over generations (E) as the primary goal, with other types of selection either eliminated (e.g. applying irrigation to eliminate drought selection), controlled for (e.g. in experimental plot design to reduce σ_E^2), or used to optimize selection for E (e.g. roguing off-types) (Cleveland and Soleri, 2007).

Figure 14.1 focuses on selection under farmer conditions. *Natural selection* is not influenced by farmers, in contrast with human or *artificial selection*. Artificial selection is both *indirect*, a result of the environments created by farmers and plant breeders, e.g. in their fields and store rooms, and *direct*, a result of human selection of planting material. Direct artificial selection can be both unconscious or *unintentional* (based on implicit or correlated criteria), when no conscious decision is made about the trait selected for, and conscious or *intentional* (based on explicit criteria), the result of decisions to select for certain traits.

14.1.3 A biological model to compare farmer and plant breeder knowledge and practice

Many plant breeders and other outsiders who work with farmers make the mistake of assuming that western scientific knowledge and practice is always more accurate and 'better' than that of farmers. To have a way of comparing plant breeder knowledge (PBK) and farmer knowledge (FK), a neutral comparator that can function as

a bridge between these is useful (Soleri and Cleveland, 2005). For plant breeding, the most fundamental model of the relationship among phenotype, genotype and environment is assumed to be a good model of reality that is the basis for PBK; we will assume it is also the basis for FK. This model is universally accepted by biologists, including plant breeders, but they disagree among themselves about its interpretation at higher levels of generalization, for example whether selection in optimal or marginal environments leads to genotypes that are better adapted to marginal environments (Ceccarelli and Grando, 2002) (see Chapter 2). This variation in scientists' interpretations suggests that, if farmers do in fact think in terms of this basic biological model, it would be a valuable comparator, facilitating understanding of variations (differences in higher levels of its interpretation) within and between FK and PBK on equal grounds.

We use the two parts of the model on which plant breeding is based (Cleveland, Soleri, and Smith, 2000), as presented in standard texts (e.g. Falconer and Mackay, 1996: 189; Simmonds and Smartt, 1999: 193).

1. Variation in population phenotype (observable characteristics) (σ_P^2) on which choice (discrimination between different groups of plants) and selection (discrimination among individual plants within a group) are based is determined by genetic variation (σ_G^2), environmental variation (σ_E^2), and variation in genotype (genetic constitution)-by-environment ($G \times E$) interaction (σ_{GE}^2), thus $\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$.
2. Response to selection (R) for a trait is the difference between the mean of the whole population from which the parents were selected and the mean in the next

generation produced by planting those selected seeds under the same conditions. R is the product of two factors, b^2 and S ($R = b^2S$), where S is the selection differential, the difference between the mean of the selected parental group and the mean of the entire original population (Allard, 1999: 101–102; Falconer and Mackay, 1996: 189; Simmonds and Smartt, 1999: 193). Narrow sense heritability (b^2) (that part of σ_p^2 that can be passed directly from parent to progeny, the additive variance, σ_a^2) = σ_a^2 / σ_p^2 . Thus, artificial phenotypic selection *per se* is a process of identifying the individuals with specific phenotypic traits within a population that will contribute genetic material to the next generation, and is distinct from the heritability of those phenotypic traits (see Section 14.5).

In our use of the basic biological model, we make several assumptions. (1) It models empirically observable patterns in the real world. (2) Among both farmers and plant breeders and other scientists, there are some who are particularly good observers of their environments, crops and interactions between these if they occur, while others are poor observers, resulting in variation within groups. (3) Variation in knowledge within and between groups can also be caused by experiences with different genotypes and environments, and by different values and pre-existing knowledge. (4) Differences between FK or PBK and the model do not mean that either form of knowledge is wrong, and differences between FK and PBK do not mean that either is inferior to the other.

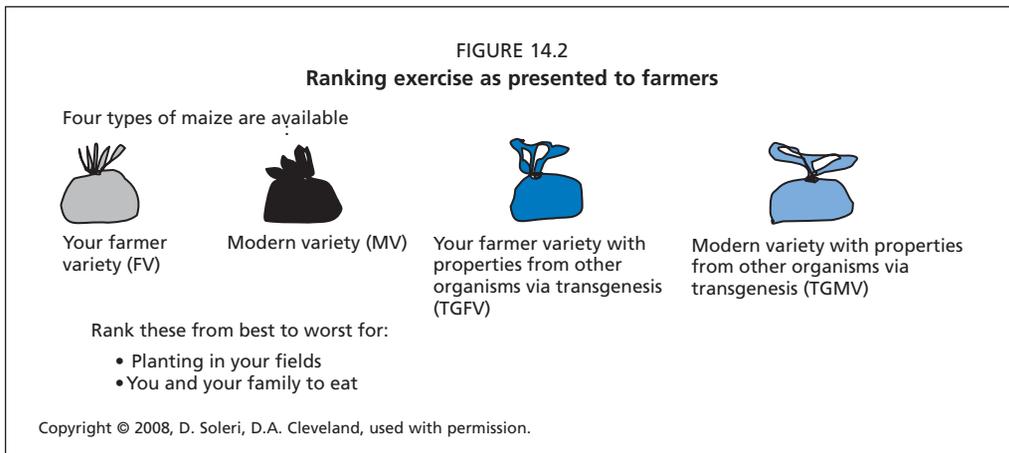
Thus, experiences under diverse circumstances can result in local interpretations of the model, by either farmers or scientists, which can be sources of learning for both scientists and farmers (Cleveland and

Soleri, 2002b). When FK differs from that presumed by plant breeders' interpretation of the model, we should try to understand the difference in terms of the specific genotypes and environments each works with, as well as other factors in their experience.

14.1.4 Methods for understanding farmers' knowledge and practice

The best starting place for collaboration may be simple interviews with a representative random sample of households. Such interviews can provide insights critical for collaboration. There are many resources available describing how to conduct such interviews (e.g. Cleveland and Soleri, 1991) and analyse them (e.g. Stern *et al.*, 2004). The key requirements are that: (i) the sample is representative of the human population with which you are working, possibly requiring a stratified sampling approach, based for example on gender of farmers, household socio-economic status, or dominant soil type on farms; (ii) people conducting the interviews are consistent, respectful, open and primarily listen to and document farmers' answers and comments; and (iii) questions are relevant for understanding and collaboration.

In addition to simple questions to elicit basic descriptive data (household size, number working in farming, area sown to each crop, sources of planting seed, yields, etc.), methods such as scenarios and ranking exercises may use hypothetical varieties to better understand farmers' theoretical knowledge, or actual varieties they are familiar with for insights into specific experiences and observations (Crossa, Bellon and Franco, 2002; Soleri and Cleveland, 2005). For example, a scenario using hypothetical maize varieties was created to better understand the G×E interaction most valued by maize farmers in a study in Mexico, Cuba and



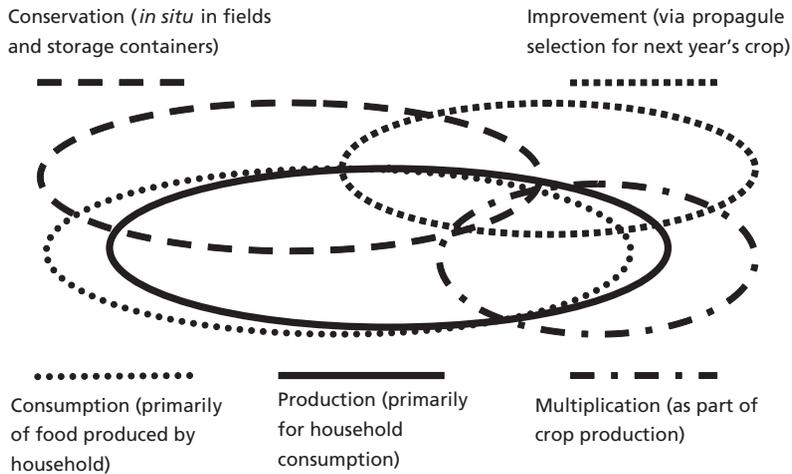
Guatemala (Soleri *et al.*, 2005). When asked to choose between two maize varieties with qualitative G×E response to annual precipitation, 61 percent of farmers preferred a variety with lower yield potential, mean and yield variation ('stable') to a variety with higher yield potential, mean and yield variation ('responsive'). The answer varied, with farmers from more difficult growing environments preferring the stable variety at a significantly greater frequency than those in more favourable growing environments. A similar scenario was created to investigate farmers' attitudes towards some of the possible consequences of pesticidal transgenes in their maize varieties and the evolution of resistance in the pests that it controlled. Some of these consequences were reliance on the formal seed system, a higher seed price and initially high but declining yields over time as pest populations evolved resistance. The hypothetical transgenic variety was not identified as being transgenic when the scenario was presented to farmers. Of those interviewed (n = 334), 70 percent chose a lower yielding but more stable and locally available variety (Soleri *et al.*, 2005). Similarly, an exercise asked those farmers to rank four types of maize: their own FV, a conventional MV they were familiar with,

and those same varieties as backgrounds for a transgene: a transgenic farmers' variety and a transgenic modern variety (Figure 14.2). We asked farmers to rank these first as maize seed for sowing in their own fields, and then again as maize grain for their family to eat. The FV and MV represented two seed systems (informal vs formal, respectively) and had different agronomic, storage and culinary characteristics with which farmers were already familiar. Farmers had no previous experience with transgenic crop varieties (TGVs). Providing these four choices allowed us to distinguish farmers' preferences for varieties or genetic backgrounds (FV vs MV) from their preference for a genetic technology (TGV vs non-TGV), an important distinction that is either overlooked or confounded in most research with farmers. TGVs were described neutrally to farmers and they were given a positive example of TGVs with the potential to decrease pest damage.

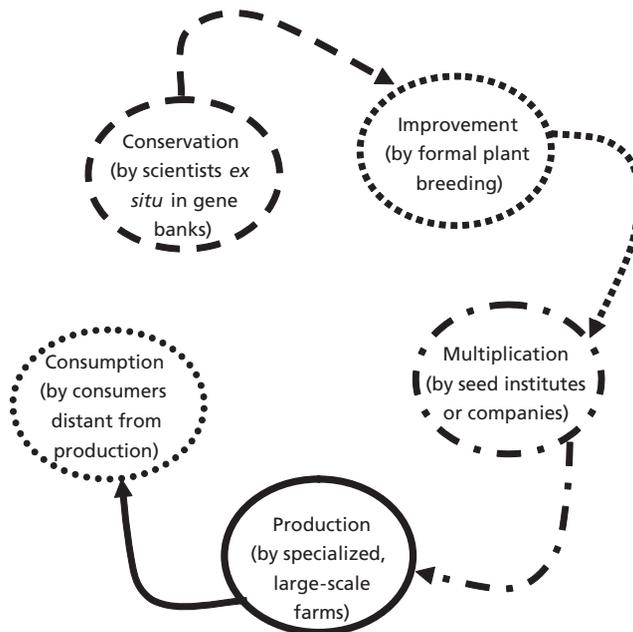
14.2 THE CONTEXT: INDUSTRIAL AND THIRD WORLD AGRICULTURE

Industrial and Third World agriculture are different in important ways in terms of seed and food systems, growing environments and crop genotypes. They are also similar in

FIGURE 14.3
Components of agricultural systems in traditionally-based small-scale and industrial large-scale agriculture



a. Traditionally-based agricultural system: functions integrated in households and communities



b. Industrial agricultural systems: functions separated, specialized, many institutionalized

terms of the basic principles and processes governing these variables and the interactions among them, including the outcome of choice and selection. Better understanding of these differences and similarities, and their relationship to differences and similarities between farmers' and breeders' goals, knowledge and practices, can help to further collaboration between farmers and plant breeders.

14.2.1 Seed and food systems

In industrial agriculture, food production, food consumption, crop improvement, seed multiplication and crop genetic resources conservation are specialized, physically and structurally separated, and farming is often considered to be primarily a business (Lyson, 2002) (Figure 14.3a). In SSTW agriculture these functions are combined within the farm household and community (Figure 14.3b) (Soleri and Cleveland, 2004), as described below. The differences due to separation vs integration of these critical functions in seed and food systems have important implications for decisions about the best ways for farmers and breeders to improve yields and quality traits, and to minimize farmers' risk.

Production

SSTW agriculture is essential for feeding a significant proportion of the world population now, and will probably remain so in the future, even with production increases in large-scale, industrial agriculture (Hazell *et al.*, 2007; Heisey and Edmeades, 1999). As mentioned earlier, over 2 billion people live on almost half a billion small-scale farms (<2 ha) in the Third World, including half of the world's undernourished people and the majority of those living in absolute poverty (Nagayets, 2005). Food production relies on household labour, and most house-

holds sell some portion of their production in the market, but they are incompletely integrated into these markets (Ellis, 1993). Farmers' production knowledge combines understanding based on theory and empirical observation with values about the social and cultural significance of farming, often focused on FVs (Soleri *et al.*, 2002).

Off-farm income is often critical for households' overall survival strategy, and may reduce the importance of on-farm production. Migration of household members, for example, may lead to labour shortage (Narayanan and Gulati, 2002) and to reduced time and other resources devoted to seed selection, conservation of crop genetic diversity or production, and eventually to loss of the knowledge on which they depend (for an example in central Mexico, see Fitting, 2006).

Consumption

Farm families rely on their own food production for a significant proportion of their food, and FVs are valued for traits that contribute to storage, food preparation, taste, colour, texture and specific uses (e.g. maize varieties grown for husks used in tamale production) (Soleri and Cleveland, 2001), or sticky rice FVs used for traditional foods in southern China (Zhu *et al.*, 2003). These specialized uses mean some FVs have high market values.

Improvement

Cultivation in new locations, farmers' changing selection criteria and growing environments were responsible for the tremendous increase in intraspecific crop diversity via mass selection following domestication (Harlan, 1992; Matsuoka *et al.*, 2002) (see Chapter 1, this volume), and all of these continue today. It has been best documented at a local level in vegetatively

propagated crops (Elias *et al.*, 2001), but also in predominantly self-pollinated crops such as rice (Dennis, 1987; Richards, 1986). For cross-pollinating crops like maize, farmers may not be interested in changing quantitative phenotypic traits of their varieties through selection, but rather in maintaining qualitative traits of interest (Pressoir and Berthaud, 2004b), and can do so successfully even in the presence of high rates of gene flow at other loci (Louette, Charrier and Berthaud, 1997; Pressoir and Berthaud, 2004a). Quantitative improvement in such species may more often be sought through choosing new varieties or populations, as discussed below.

Seed multiplication

Farmers do not usually distinguish seed multiplication from food production, although sometimes they plant separate seed multiplication plots, as do some rice farmers in Sierra Leone (Richards, 1986: 138–144). Farmers often save a high proportion of their seed from their own harvests, but often also obtain seed through informal seed systems (Ndjeunga, 2002), and frequently experiment with new seed (Louette, Charrier and Berthaud, 1997), including planting seed obtained as grain (Soleri *et al.*, 2005). The result is extensive gene flow via seed and other propagules, as well as by pollen flow, creating seed systems that are predominantly local and genetically open (Berthaud *et al.*, 2001; Pressoir and Berthaud, 2004a; vom Brocke *et al.*, 2003a).

Conservation

Farmers conserve crop genetic diversity of FVs *in situ* in their fields and storage containers (Qualset *et al.*, 1997). Most *in situ* conservation is done indirectly—perhaps unintentionally—as a result of

using or selecting and saving FV seed each year for planting (Louette and Smale, 2000; Soleri, Smith and Cleveland, 2000). This conservation is dynamic in that populations are exposed to changing natural and artificial selection pressures, often creating locally distinct and adapted populations through indirect selection.

Because food production and consumption and crop improvement, seed multiplication and conservation are all carried out within the same crop population, that population will not be optimized for any one function *per se* as it might be in industrialized systems. For example, the value of FV genetic diversity in its local conservation role may in some way be in conflict with the genetic composition ‘optimal’ for its role as an improved population (Soleri and Smith, 1995). In this sense, farmers’ crop populations are similar to semi-natural plant populations that

...approach complex equilibria in which overall fitness is as high as the varied demands of differing sites and seasons, complex genetic control and the long term demands of adaptability allow.

(Simmonds and Smartt, 1999: 91)

For this reason, and because of the value of this farming for production and dynamic conservation, both *in situ* conservation by farmers and *ex situ* conservation in formal gene banks are necessary and complementary. However, for conservation to play a useful role, interaction between farmers and scientists is required, e.g. to ensure that the selection environments in *ex situ* conservation do not result in evolution that makes the population unsuitable for farmers in the event that they require renewal of their seed from outside their communities (Soleri and Smith, 1995). In a similar way, collaboration between farmers and

plant breeders needs to balance the goals of the breeder, which will tend to focus on improving specific traits, with the other functions of the food and seed system.

14.2.2 Growing environments and genotypes

Growing environments and crop genotypes of Third World farmers differ in important ways from those with which most plant breeders and agronomists in industrial countries are familiar. Farms often consist of a number of small, scattered fields with marginal growing environments, i.e. relatively high levels of stress and of temporal and spatial variability. For example, while the average size of maize grain farms in the United States of America in 2003 was 79.2 ha (USDA NASS, 2004), in the southern Mexican state of Oaxaca over 76 percent of maize farms were smaller than 5 ha in 1995 (INEGI, 2001), and in one of the communities in the Central Valleys of Oaxaca where we have worked, the average farm size is 3.7 ha and the average maize field size is 0.8 ha (Soleri, 1999; Soleri, Cleveland and Aragón Cuevas, 2003). In that same Oaxacan community, coefficients of variation of maize yields calculated using triangulation of farmer estimates were very high, averaging 44 percent (Soleri *et al.*, n.d.). Indeed it has been estimated that maize farmers in that area of Oaxaca experience production failure one year in four due to drought (Dilley, 1997). In addition to high levels of environmental variability, other factors contribute to high levels of yield variability and production risk. SSTW farmers typically use low levels of external inputs, and have limited access to government programmes and markets, and limited influence on the policies affecting them (Ellis, 1993; Hardaker, Huirne and Anderson, 1997).

For many plant breeders who work

with farmers, this environmental stress and variation mean that selection for improved performance in farmers' environments needs to take place in those environments, and requires re-thinking some of the assumptions of conventional plant breeding (Ceccarelli and Grando, 2002). However, many plant breeders, especially those with little experience with farmers' growing environments, believe that as a general principle selection should be done in optimal environments because there are 'spillover' effects to marginal environments (for discussion, see Atlin *et al.*, 2000; Rajaram and Ceccarelli, 1998). Thus, while plant breeders agree on the basic principles of selection, they can disagree vehemently about how those principles should be applied to farmers' environments (Ceccarelli and Grando, 2002; Cleveland, 2001). One source of such disagreements may be differing interpretations of empirical observations and theories thought to underlie them (see Section 14.2.3).

Farmers often continue to use locally selected FVs, even when MVs produced by the formal plant improvement and seed multiplication systems are available, because FVs may be better adapted to marginal growing environments, and because MVs may be agronomically, culinarily and economically inappropriate (Ceccarelli *et al.*, 1994; Evans, 1993; Heisey and Edmeades, 1999). Farmers value FVs for agronomic traits, such as drought resistance, pest resistance and photoperiod sensitivity, as well as for traits contributing to storage, food preparation, taste, market value and appearance (Smale, 2002). FVs include landraces, traditional varieties selected by farmers, MVs adapted to farmers' environments by farmer and natural selection, and progeny from crosses between landraces and MVs (sometimes

referred to as ‘creolized’ or ‘degenerated’ MVs) (Zeven, 1998; FAO, 1996).

FV yields are often much lower in the Third World compared with MV yields in industrialized agriculture, e.g. maize yields in United States of America (~8 t/ha) compared with Mexico (~2 t/ha) (Aquino *et al.*, 2001) and Oaxaca (~0.8–1.5 t/ha) (Aragón-Cuevas *et al.*, 2006). However, yield stability is often greater with FVs than for MVs grown in the same environments, because MVs often have steep response regression curves, i.e. are highly responsive to marginal environments, as well as optimal ones (Ceccarelli, 1997; Evans, 1993).

An important reason for the higher yield stability of FVs is their higher level of genetic diversity compared with most MVs, presumed to support broad resistance to multiple biotic and abiotic stresses (Brown, 1999). In addition, many centres of origin and centres of diversity for crop species are in the Third World and cultivated primarily by small-scale farmers, thus SSTW agriculture is an important reservoir of genetic diversity in the form of FVs (FAO, 1996). This diversity makes FVs valuable not only for farmers, because they decrease the production risks in marginal environments, but also for the *in situ* conservation of crop diversity as a source of resources for breeding MVs.

14.2.3 Plant breeder knowledge

As outlined above (Section 14.1.3) the basic model of plant genotype-environment interactions are well established and universally accepted by plant breeders. However, many complexities of that model are still not well understood in terms of biological theory (Duvick, 2002), and there continue to be disagreements about the interpretation of the basic model and its implications for practice among plant breeders, such as the effect of selection environment on

the range of target environments to which a genotype is adapted (Atlin *et al.*, 2000; Bänziger and de Meyer, 2002; Ceccarelli and Grando, 2002).

In specific situations, understanding this basic theory is difficult because a great number of variables affect it, and predictions are hampered by the lack of experimental data and lack of the technologies and resources necessary to gather and analyse them. Plant breeders recognize that their theoretical understanding of plants beyond the basics is limited, and that much plant breeding has been based on intuition and empiricism rather than theory (Duvick, 1996; Simmonds and Smartt, 1999; Wallace and Yan, 1998), although intuition and empiricism are likely to be underlain to a lesser or greater extent by the basic theoretical understanding of genotype x environment relations.

This fundamental biological theory is the same no matter where plant breeding is practised. However, the biophysical, economic and sociocultural variables through which this and other theories work can be quite different. For example, think of the contrast between farmers’ fields in marginal environments and plant breeders’ research stations, or between national agricultural policy priorities of large-scale efficiencies and increased inputs and production, and farmers’ priorities of reducing risk and optimizing crop production as part of a general household survival strategy. Work under a specific set of circumstances may lead to interpretation of theory that is then generalized and broadly applied, without investigating the validity of those interpretations under all circumstances. For example, the fundamental principle that—all else remaining constant—as σ_E^2 decreases, h^2 increases has been interpreted to imply that selection in low σ_E^2 environments provides

the best response for all environments, including ones with high σ_e^2 . However, empirical testing has shown this not to be true in many cases (e.g. Ceccarelli, 1996; Ceccarelli *et al.*, 1994, 2003; Comadran *et al.*, 2008); two reasons are that, first, the genes responsible for a quantitative trait such as yield may be different in different environments (e.g. Atlin and Frey, 1990; Atlin, McRae and Lu, 2000; Venuprasad, Lafitte and Atlin, 2007), and, second, b^2 of some important traits may not be entirely obscured by σ_e^2 (Al-Yassin *et al.*, 2005) (see Chapter 2, this volume). Working with farmers often requires that breeders test the validity of those interpretations of theory that form the basis of conventional plant breeding. This includes comparing the genotypes and environments and goals for improvement, and testing the assumptions (biological, environmental, economic, sociocultural) on which they are based, and adjusting interpretations of theory, and hence methods used (Ceccarelli and Grando, 2002).

For this reason, farmer–breeder collaboration may often benefit from making a clear distinction between (a) fundamental biological theory, (b) interpretations of fundamental theory, and (c) methods and practice, with ‘c’ possibly very different depending on whether it is based on ‘a’ or ‘b’, or on different versions of ‘b’. Many of the disagreements about plant breeding methods for participatory plant breeding (PPB) may grow out of disagreements about differences in the *interpretation* of fundamental biological theory, and disagreements about these interpretations may in turn be based on the belief of proponents that their interpretations of fundamental theory are *not* based on their unique experiences and assumptions, but rather are part of fundamental theory.

Therefore, especially for those biophysical aspects of genotypes and environments that are less well understood in terms of plant breeding theory, PBK may more likely to be based on each person’s or institution’s specific experiences with the particular environments and crop genotypes they work with, and thus may be less generalizable, and more apt to be influenced by pre-existing knowledge (including values) specific to the plant breeder’s social environment. This means that disagreements between farmers and plant breeders, and among plant breeders, could arise even though fundamental genetic and statistical principles remain constant across a range of contexts, because the ‘art’ of plant breeding is more tied to specific individuals or environments (Ceccarelli and Grando, 2002; Soleri and Cleveland, 2001).

14.2.4 Farmer knowledge

A lack of empirical research and theoretical analysis has contributed to using overly simplified definitions of FK (and often of PBK as well), and the common failure to test the many assumptions underlying these definitions (Cleveland, 2006; Sillitoe, 1998). We can very roughly divide current views of FK into two categories: there are those that see FK as fundamentally different from PBK, and those that see it as fundamentally similar. These views also form the basis of particular advocacy perspectives; generally neither considers the theoretical content of FK.

In the first category, definitions of FK emphasize that it is primarily value-based, comprising intuition and skill, socially constructed, and based on the local social and environmental contexts and culture. According to this perspective, farmer and PBK are seen as fundamentally different, and attempts to explain FK in scientific terms impede true appreciation of FK.

The second category emphasizes that FK consists primarily of rational empirical knowledge, usually focusing on either economic or ecological knowledge. Definitions of FK as economically rational tend to assume that scientists are more rational, and that farmers are risk neutral and their behaviour is based on a desire for profit maximization in the form of high average yields (e.g. Zilberman, Ameden and Qaim, 2007). According to this definition, the role of outsiders should be to facilitate the replacement or modernization of small-scale farming, including replacement of FVs with MVs (Mohapatra, Rozelle and Huang, 2006; Srivastava and Jaffee, 1993). The definition of FK as ecologically rational tends to assume that farmers have detailed, accurate and therefore sustainable ecological knowledge of their environments. The first part of that definition is supported by much empirical data, especially ethnotaxonomic studies of plants and animals, while recognizing variation in distribution of cultural knowledge as the result of factors including age, gender, social status and affiliation, kinship, personal experience and intelligence (Berlin, 1992).

Participatory research has usually been based on the second definition of FK. As a result, the focus in using farmer knowledge has been on the details it can provide in the form of a discriminatory or, most frequently, descriptive tool in PPB. For example, a major survey of 49 PPB projects found that the primary focus was soliciting farmers' descriptions and rankings of selection criteria. For about two-thirds of these projects, "identifying, verifying, and testing of specific selection criteria was the main aim of the research", and 85 percent obtained farmers' selection criteria for new varieties (Weltzien *et al.*, 2003: 17–18, 51, 75). The main impact on scientific plant breeding

appears to have been "better understanding of new ideotypes based on farmers' experiences, specific preferences and needs" that will affect priorities of formal plant breeding and the "process of formal variety development" (Weltzien *et al.*, 2003: 75).

More recently, using FK of crops as a discriminatory tool has become more common. This has been important in some PPB work, with farmers asked to choose among varieties already released in other areas (e.g. for rice and chickpea; Joshi and Witcombe, 1996), among new and experimental varieties (e.g. for pearl millet; Weltzien *et al.*, 1998), or among segregating populations (e.g. F₃ bulks with barley; Ceccarelli *et al.*, 2000), or to select individual plants within segregating populations (e.g. F₅ bulks of rice; Sthapit, Joshi and Witcombe, 1996; and F₄ bulks of rice; Virk *et al.*, 2003). When such choice or selection is accomplished using actual plants, plant parts or propagules, analysis of results can reveal farmers' implicit criteria that they may not be able to verbalize easily, if at all (i.e. it may be unconscious) (Louette and Smale, 2000; Soleri, Smith and Cleveland, 2000).

These approaches to understanding FK have made valuable contributions to achieving more effective crop improvement for farmers' conditions. However, the theoretical basis of FK is not usually considered, and rigorous comparisons with PBK have not been carried out, "opportunities rarely develop for interaction between breeders and farmers beyond the survey", with the discussion "driven by the breeders' concepts of the present situation, making it difficult for farmers to express their views in the context of their reality" (Weltzien *et al.*, 2003: 51). It may also be difficult for farmers to communicate to outsiders their knowledge that goes beyond description or discrimination. For this reason a

definition of knowledge—both farmer and scientist—as complex, and including values, empiricism, theory and experience is useful (Cleveland, 2006). This definition underlies an approach that starts with basic theoretical knowledge and clearly distinguishes theory from its local interpretation, in an attempt to better understand farmers' choice and selection, and to identify possible bases for substantive collaboration between farmers and scientists. In the rest of this chapter we use this definition to look at two key processes in plant breeding: choice of populations (or varieties) for direct use or for further breeding, and selection of individuals within a population. We focus on our understanding of FK and practice of choice and selection, how farmers and scientists can better collaborate in those steps, and why such collaboration is important.

14.3 FARMER CHOICE AND SELECTION: PAST, PRESENT AND FUTURE

While this chapter is primarily about contemporary farmer and plant breeder choice and selection, a brief look at the broad trends in the past, present and future of crop improvement in relation to farmers will help in understanding the challenges and potential for plant breeding with farmers. This section is not essential for understanding the rest of the chapter, and might be quickly skimmed and used as a reference.

As measured by the rate of desired crop genetic changes achieved by selection, three broad stages have been suggested (Gepts, 2004). Initial rapid progress with domestication was followed by long periods of much slower change as original domesticates spread to new environments and responded to a range of new natural and artificial selection pressures, and with modern plant breeding the rate of change in MVs increased substantially, while most

farmers continued as before. There have also been marked changes in crop genetic diversity over time, especially at specific and intraspecific taxonomic levels.

14.3.1 Domestication and subsequent changes in diversity

While domestication resulted in a large decrease in the number of plant species exploited, it was followed by large increases in intraspecific diversity, as FVs evolved as a result of natural and artificial selection in new biophysical and sociocultural environments (Harlan, 1992) (see Chapter 1, this volume). For many of the more widely grown food crops, domestication resulted in evolutionary changes making them genetically distinct from their closest wild relatives today, and most became dependent on humans for reproduction (Harlan, 1992; Simmonds and Smartt, 1999). Exceptions exist, especially among some perennial fruit crops, more accurately described as semi-domesticates, where crops are not the result of selection resulting in *E*, but rather are choices of superior genotypes from among those extant in the wild (for olive, see Baldoni *et al.*, 2006, and Breton *et al.*, 2006).

Domestication seems likely to have been the result of indirect selection and unintentional direct selection (e.g. when farmers select for large seed size or brittle rachis as a result of their seed collection behaviour; Harlan, 1992), and perhaps some intentional selection for evolutionary change (see Section 14.1.2). However, it is very difficult or impossible to determine the type of selection that resulted in past crop evolution, and experts differ on the type they believe was most important. For example, Allard emphasizes direct, intentional selection,

The consensus is that even the earliest farmers were competent biologists

who carefully selected as parents those individuals ... with the ability to live and reproduce in the local environment, as well as with superior usefulness to local consumers.

(Allard, 1999)

In contrast, Simmonds and Smartt (1999: 13) emphasize indirect selection: “the art of cultivation is perhaps the peasant’s most potent contribution.”

Similar to studies based on archaeological data, results of molecular analyses support the hypothesis that farmers’ selection has been successful in achieving evolutionary change for traits in the ‘domestication syndrome’ that might be indirectly or unintentionally favoured because of agronomic superiority (see Chapter 1, this volume). There is also evidence that farmer selection has been a powerful force for evolutionary change based on other preferences as well. For example, three major genes involved in starch metabolism in maize were found to have unusually low genetic diversity compared with its closest wild relative (teosinte, *Zea mays* subsp. *parviglumis*), which is strong evidence of selection for specific processing and culinary qualities important for the primary manner in which maize has been consumed in its regions of origin and diversity (Whitt *et al.*, 2002). In addition, three other loci contributing to sweet maize grain phenotypes showed low diversity (resulting from strong selection) in only certain varieties in particular locations, evidence of further specialization in the non-agronomic selection pressures farmers have exerted on maize (Olsen *et al.*, 2006; Whitt *et al.*, 2002). Similarly, it appears that strong directional selection for sticky, glutinous grain quality resulted in a selective sweep affecting an area over 250 kb long that includes the locus coding for this quality (low amylase produc-

tion) and other linked loci. The presence of this sweep distinguishes the sticky rice favoured by upland northeast Asian peoples from the non-glutinous rice varieties used by other Asian groups, and presumably would be among their fundamental choice criteria, perhaps as an adaptation for eating with chopsticks (Olsen *et al.*, 2006).

Increasing evidence for a number of crops suggests that domestication could have occurred over short periods relative to the ~12 000 years that crop plants have been cultivated (Gepts, 2004). Domestication syndrome traits often appear to be determined by a small number of genes with large effects, suggesting that domestication could proceed relatively rapidly. For example, Paterson *et al.* (1995) found a small number of quantitative trait loci (QTLs) coding for the domestication syndrome traits of seed size, photoperiod sensitivity of flowering, and brittle rachis in taxonomically distinct cereals with diverse centres of origin (sorghum, rice and maize). In common bean (*Phaseolus vulgaris* L.), control of the domestication syndrome involves genes that have a large effect (>25–30 percent) and account for a substantial part of the phenotypic variation observed (>40–50 percent) (Koinange, Singh and Gepts, 1996). Simulations based on sequence variations at loci coding for biochemical or structural phenotypes in maize and its close and distant relatives have estimated that domestication could have taken from 10 (Eyre-Walker *et al.*, 1998) to between 315 and 1 023 generations (Wang *et al.*, 1999). In addition to selecting for characteristics of the ‘domestication syndrome’, especially in cereals and small pulses (Harlan, 1992), domestication in sexually propagated crops may have resulted in increased autogamy and therefore homozygosity, expressed

phenotypically in greater trueness to type in a population over generations. In contrast, some vegetative propagation may have selected for heterozygosity (via heterosis) and therefore for allogamy, as contemporary evidence suggests for cassava (Pujol, David and McKey, 2005).

The genetic changes that define crop domestication are inextricably linked with changes in selection pressure. These pressures are not only exerted by direct human selection of propagules for planting, but perhaps more often with the differences in selection pressures created by human modification of growing environments (Figure 14.1). In southeast China, for example, evidence for the earliest cultivation of both wild and domestic rice (~7 700 BPE) suggests that this occurred where farmers were intensively managing coastal wetlands with fire to control vegetation and bunds to control flooding, and increased nutrient concentration in fields (Zong *et al.*, 2007). Bringing wild plants into human modified environments, such as compost heaps near houses, as well as exchange of seeds and other propagules, also facilitated domestication via hybridization, as with *Leucaena* in southern Mexico, and probably with two other important domesticates from that region, agave (*Agave* spp.) and prickly-pear cactus (*Opuntia* spp.) (Hughes *et al.*, 2007). Domestication generally decreased the fitness of plants in natural environments, and made them more dependent on humans and human-managed environments.

The geographical spread of domesticated crops led to great varietal diversification as a result of the increase in diversity of natural and artificial selection pressures encountered, followed by choice among preferred populations. It is generally assumed that simple mass selection by

farmers working in combination with local natural selection contributed to the large amount of intraspecific diversity that evolved following domestication:

Probably, the total genetic change achieved by farmers over the millennia was far greater than that achieved by the last hundred or two years of more systematic science-based effort.

(Simmonds and Smartt, 1999: 12).

14.3.2 Modern, scientific plant breeding

Farmer and plant breeder crop improvement began to be separated about 200 years ago in “technically advanced temperate countries” (Simmonds and Smartt, 1999: 12) with the beginning of specialized, amateur breeding. The widespread acceptance of evolution and the rediscovery of Mendel’s research after 1900 eventually led to modern scientific plant breeding, based on a combination of Darwinian evolution, Mendelian genetics and biometry (Fitzgerald, 1990; Provine, 1971), with modern plant breeders considering themselves ‘applied evolutionists’, whose goal is to develop plant varieties better adapted to growing environments, measured primarily as increased yield (Allard, 1999).

Farmers and formal plant breeders continued to collaborate at this time, for example in making crosses and selections in maize breeding in the United States of America (Fitzgerald, 1990; Schneider, 2002). But as the importance of evolutionary theory in plant breeding increased in comparison with empirical heuristics, the economic importance of plant breeding increased and came to dominate formal plant breeding by professional plant breeders. Simultaneously, the farmer’s role in crop improvement in industrial countries decreased, for example in the United States of America (Fitzgerald,

1990; Kloppenburg, 1988) and Switzerland (Schneider, 2002). Plant breeders' concepts subsequently developed independently of farmers' concepts, effectively separating the formal from the informal systems of crop improvement and seed multiplication. When farmers are involved by contemporary plant breeders in their work it has generally been limited to the stage of evaluating and choosing among plant breeders' populations or varieties in their fields (Duvick, 2002).

14.3.3 Biotechnology

Advances in genetics and molecular biology have led to developments in biotechnology that have dramatically enhanced the ability to understand and manipulate plant genomes. Functional genomics has elucidated the relationship among genetic components and to phenotypes; marker assisted selection (MAS) has increased the efficiency of breeding for specific traits; and genetic engineering has made it possible to transfer genes from almost any organism into a crop species. When these genes come from a different species the process of transformation is called transgenesis, and the resulting crop variety a genetically engineered (GE) variety, genetically modified organism (GMO) or, most accurately, a transgenic crop variety (TGV).

TGVs are a rapidly growing agricultural technology, with the area planted increasing by 9.4 percent from 2007 to 2008, to over 125 million hectares (James, 2006, 2008), or over 9 percent of cultivated land globally (calculated from FAO, 2007, 2009). Currently grown TGVs are primarily targeted to industrial agriculture and designed to enhance yield and net profit for farmers by directly reducing pest damage or facilitating herbicide use. Globally, most of the area planted to TGVs is in large-scale

industrial agriculture, and is expanding in the Third World. Of the 23 countries growing TGVs in 2007, 12 were 'developing' countries, and estimated to account for 43 percent of the area planted and 90 percent (11 million) of the farmers growing TGVs. Of these, 99 percent (10.9 million) were in China and India, growing mostly Bt cotton (James, 2006, 2007). Currently, TGVs of food crops for Third World farmers are either planned, being developed, in field trials, or approved and in production.

TGVs are currently being promoted by development organizations, governments and corporations as the key to increasing production and income and reducing hunger and malnutrition in SSTW agriculture (FAO, 2004; Rockefeller Foundation, 2007; World Bank, 2007). However, the focus on TGVs to improve Third World agriculture is very controversial (Abate *et al.*, 2008; Stokstad, 2008). A number of studies, mostly by economists and of Bt cotton, maize and rice, have concluded that farmers readily adopt TGVs because they increase yield and income, reduce pesticide applications or improve farmer health (Gouse *et al.*, 2006; Huang *et al.*, 2003, 2005; Morse, Bennett and Ismael, 2006; Qaim and Zilberman, 2003). Other studies have found that adoption may be the result of fads (Stone, 2007) or a lack of freedom to choose (Witt, Patel and Schnurr, 2006), and that higher yields and reduced pesticides may be reversed after several years due to the emergence of secondary pests (Wang, Just and Pinstrup-Andersen, 2006). Others have suggested that the net benefits of TGVs may not be as great as those of alternative improvements in agriculture (e.g. Uphoff, 2007). The potential ecological and genetic effects of TGVs and transgene flow into non-TGV crop or wild or weedy populations, especially in Third

World agriculture, are not well understood (Ellstrand, 2003b; Heinemann, 2007; NRC, 2002; Snow *et al.*, 2005).

The spread of biotechnology has also resulted in unintentional transgene flow, including into centres of diversity, e.g. maize transgenes documented in Mexican FVs (Alvarez-Morales, 2002; Pineyro-Nelson *et al.*, 2009; Serratos-Hernández *et al.*, 2007). Such transgene flow can be difficult to prevent (NRC, 2004), the early stages of transgene flow to FVs are extremely difficult to monitor (Cleveland *et al.*, 2005), and the effects may often be irreversible (Ellstrand, 2003a). Potential effects of transgene flow on FVs and farmers are both positive and negative, and will require risk analysis and evaluation specifically adapted to each location – crop combination within the Third World (Cleveland and Soleri, 2005; Soleri, Cleveland and Aragón Cuevas, 2006). Transgenes can introduce novel forms of diversity into the crop populations being selected upon by farmers and plant breeders, but there is no reason to expect that farmers will be able to retain, discard or manipulate them any differently from other genes.

14.3.4 Privatization

In the early 1980s, some countries and farmer support groups sought to do away with all intellectual property rights (IPRs) in crops, establishing 'farmers' rights' to all crop genetic resources, but this move was defeated by the United States of America and other industrial nations (Fowler, 1994), and private rights in plants and other living organisms now dominate, with industrial patents leading the way (Atkinson *et al.*, 2003). Farmers were left with having to defend themselves from the advances of an IPR system in plants designed by industrial nations and corporations, a system that generally does not recognize farmers'

traditions or current needs (Cleveland and Murray, 1997).

Much plant breeding has moved from the public to the private sector (Frey, 1996) and thus selection criteria are increasingly vulnerable to being dominated by private profit motives rather than public good motives (Simmonds, 1990), which is especially evident for TGVs. The major share of agricultural biotechnology processes and products are controlled by private multinational corporations with little incentive to develop TGVs most appropriate for Third World farmers who cannot afford to pay the premium for TGV seed (CGIAR, 2006; World Bank, 2007: 178).

Similarly, there is increasing concentration in the seed sector, which potentially reduces competition and limits the kinds of crops and crop varieties produced and made available. The largest seed companies control an ever larger proportion of the seed market; according to one estimate, between 1997 and 2004 the companies with the largest sales increased their market share from 27 percent to 33 percent, and in 2004 the top four companies owned 38 percent of biotechnology patents (World Bank, 2007: 135–136).

The drive to globalize industrial-world IPRs in plants has been intensified as a result of pressure from agricultural biotechnology corporations (Graff *et al.*, 2003; Shorett, Rabinow and Billings, 2003). This means that as patented TGV crops and their transgenes move intentionally or unintentionally around the world, so could the rights of the companies who own them. Movement of transgenes into non-transgenic crop populations, whether producing a net benefit for the farmer or not, makes farmers vulnerable to IPR claims from the technology developer. In the United States of America and many other industrialized countries, patent

holders have rights to seek damages from farmers who end up with patented genes in their crops, even though farmers do not want them, and do not know they are there (Janis and Kesan, 2002). The World Trade Organization (WTO) seeks worldwide uniformity of laws for IPRs in plants and plant DNA to facilitate global enforcement, and many Third World countries have adopted the industrial world model (UPOV – International Union for the Protection of New Varieties of Plants) while others have adapted their national laws to protect small-scale farmers (World Bank, 2007: 167). The spread of IPRs and coupled economic control of agricultural biotechnology means that Third World farmers and the nation states they live in will have a difficult time gaining meaningful control of the means to intentionally create TGVs more suited to their own needs, if this is the path they choose. As a result, most organizations promoting TGVs more suited to Third World farmers are advocating public-private partnerships (CGIAR, 2006; FAO, 2004; World Bank, 2007), yet it is not clear how farmers' rights will fare in this collaboration, and they are not being rigorously addressed.

While most corporations deny they would enforce their IPRs against Third World farmers, there are no guarantees. In addition to transgenes, control of local farmers' crop genetic resources, and the traditional names and other cultural property that go with them through industrial IPRs, can legally and economically prevent local people themselves from reaping potential benefits in a global marketplace increasingly interested in traditional crops and foods (Soleri *et al.*, 1994). There are already cases of this, some of which are being challenged (Pallotini *et al.*, 2004).

14.3.5 Sustainability and farmer-scientist collaboration

The search for sustainability provoked by negative environmental impacts of agriculture (Matson *et al.*, 1997; NRC, 2002; Tilman *et al.*, 2002), and its genetic vulnerability (NRC, 1991) has led to the incorporation of more genetic variation within and among varieties by the formal crop improvement system (Cooper, Spillane and Hodgkin, 2001; Ortiz *et al.*, 2007). It has also encouraged a re-evaluation of G×E in crops and how best to exploit this for farmers' conditions (Ceccarelli *et al.*, 1994, 2001). The impact on farmer selection will be in the greater intraspecific and intravarietal diversity deployed in formally developed varieties, and greater interest in that system for breeding goals more similar to those of farmers. Part of the interest in sustainability (environmental, economic and social) has led to collaboration between farmers and scientists.

Participatory or collaborative plant breeding is attempting to reverse the separation of farmers and scientists and improve the outcomes of choice and selection in farmers' terms (Cleveland and Soleri, 2002a; PRGA, 2004; McGuire, Manicad and Sperling, 2003; Weltzien *et al.*, 2003). To that end, the next sections focus on understanding farmers' choice and selection, and thereby enabling farmers and scientists to work more closely and productively in improving the crops they grow and depend upon.

14.4 CHOICE OF GERMPLASM

It is important for plant breeders to understand how and why farmers choose varieties of their crops, because farmer choice will ultimately determine whether a new or improved variety will be useful. In this section we consider choice based on perceived

risk and yield stability, and on other factors, including quality traits.

Just as there are factors favouring the inclusion of more than one variety in a farmer's crop repertoire, there also are factors limiting the number of varieties chosen. These include farmers' resources, growing environments and crop reproductive biology, among other possible factors. Additionally, if crop varietal diversity is maintained at a community instead of household level, then farmers may not feel the need to maintain some varieties themselves each year, even though they consider those varieties to be part of their varietal repertoire and intend to grow them in the near future (for the case of rice, see Dennis, 1987).

14.4.1 Varietal choice, yield stability and risk

In much of the past plant breeding for SSTW farmers, it was assumed that high yielding varieties selected in more optimal environments would outyield FVs in farmers' environments (Ceccarelli *et al.*, 1994; Ceccarelli, Grando and Booth, 1996). If farmers did not adopt these varieties it was assumed that they were ignorant of how to improve their growing environments (Aquino, 1998), or if they could not afford to do so, it was assumed that they should get out of farming. Consideration of risk provides a different understanding of farmers' varietal choices and other practices. In the conventional economic model, a risk-neutral farmer would only grow the one variety that gives the highest profits per unit area (Smale, 2002). However, many small-scale farmers in marginal environments are risk averse (Anderson and Dillon, 1992; Soleri *et al.*, n.d., 2008), and spatial environmental variation increases the likelihood of cross-overs in varietal performance (qualitative G×E; see Section 14.5.1, below) between

farmers' fields, or even within a field (Soleri *et al.*, 2002). Variation in time is also large: in the semi-arid tropics, seasonal and annual rainfall is highly variable, and even in years with adequate total rainfall, rains may arrive late, end too early, stop for a period or be too heavy during flowering or harvesting. Therefore farmers may often grow two or more varieties of many crops, each with distinct agronomic characteristics presumably "as a measure of insurance against vagaries of the weather, diseases, or pests" (Doggett, 1988).

Understanding farmers' choice can provide valuable insights for scientific plant breeders. In response to climate change in the form of the southern movement of isohyets, policy-makers in Mali argue that improved short-cycle varieties are a critical part of stabilizing the country's volatile cereal production (Dembélé and Staatz, 2000). One result is that both sorghum breeders and farmers in southern and central Mali look north for shorter cycle varieties. Interviews in four villages in the Upper Niger River valley zone of Mali found the most common reason for adoption of the three most popular sorghum varieties was early maturity (Adesina, 1992). However, since in good rainfall years long-cycle varieties generally have higher yields (Adesina, 1992) and are rated higher for quality (Ingram, Roncoli and Kirshen, 2002), farmers do not give these up entirely. Their choices thus increase the number of varieties in their repertoires, although the net impact on genetic diversity has not been investigated. Another study in Mali of farmers' choices among their traditional sorghum varieties in terms of one or more than one variety, and short-cycle or long-cycle varieties, found that farmers make these choices in an effort to optimize outputs in the face of variation in the growing environment and in

availability of human-managed inputs, such as labour and tools. For example, better rains in 2002 compared with 2001 appear to be a major factor in the general shift toward a greater number and longer cycle length of varieties, with 60 percent of farmers adding varieties between 2001 and 2002 (Lacy, Cleveland and Soleri, 2006).

The need for research on farmer choice and risk is also illustrated in the case of potato in the Andes (Zimmerer, 2002). An emphasis on potato varieties with large tubers because farmers prefer the higher yield of these varieties would ignore the fact that poorer farmers actually select small tubers for planting because they can reduce the amount of potential food used for planting material. An implication is that the varieties poor farmers would actually choose to plant may be quite different from that anticipated by breeders, indicating changes were needed to make improvement programmes more relevant for those farmers' needs.

These and other studies suggest that crop improvement programmes need to specifically target farmers' growing environments and needs, and use local germplasm as the basis for this (Ceccarelli and Grando, 2002). They indicate the importance of plant breeders supporting varietal portfolios (Ceccarelli *et al.*, 2003; vom Brocke *et al.*, 2003a; Weltzien *et al.*, 2003) available through farmer-to-farmer exchange as an alternative to the development of a small number of varieties for large-scale adoption. In addition to decreasing farmer risk, this strategy also supports conservation of crop genetic diversity *in situ* (Ceccarelli, Grando and Baum, 2007). However, there is also some evidence that MVs developed through participatory varietal selection can replace existing FVs, as with wheat in South Asia (Ortiz-Ferrara *et al.*, 2007). When environ-

mental variation is minimal, there may be little incentive for farmers to maintain FVs while adopting MVs in order to reduce risk due to qualitative G×E (Virk and Witcombe, 2007). Clearly, the diversity outcome of locally focused improvement programmes will depend on the specific situation.

14.4.2 Other factors influencing choice

Farmers may also choose more than one variety because of their different quality traits. For example, interviews with 599 Nigerian farmers supported the conclusion that they grow both long-cycle and short-cycle cowpea varieties: short-cycle for food grain and long-cycle for feed during the dry season when other fodder sources are scarce (Abdullahi and CGIAR, 2003). Some maize farmers in Oaxaca, Mexico, maintain varieties specifically for their coloured husks or tassels because of their aesthetic qualities, e.g. coloured husks used to wrap tamales impart their colour to them (Soleri, field notes, 1996–1999), and families who make the traditional beverage *tejate* maintain more varieties of maize, using them in its preparation (Soleri, Cleveland and Aragón Cuevas, 2008).

The number of varieties grown by farmers may also be influenced by seed source and social variables (David, 2004). In a study of Mexican maize farmers, choice of total number of varieties grown was related to household seed source. Households planting mostly their own seed chose an average of twice as many varieties in comparison with those households that obtained all their seed from non-household sources (Louette, Charrier and Berthaud, 1997). In a review of field research on farmer crop genetic resources, wealth was a common indicator for producers who cultivated more varieties compared with resource-poor producers (Jarvis *et al.*, 2000). The choice of total number of sorghum varie-

ties may be significantly related to ethnicity, as in one area of the United Republic of Tanzania, where migrant Gogo farmers from a traditional sorghum-growing region grow more than twice the number of varieties as migrant groups from maize-growing regions (Friis-Hansen and Sthapit, 2000).

14.5 SELECTION

Given the historical background outlined earlier, including the emphasis on selection as practised by scientists, we now discuss the concept and process of selection, emphasizing the contexts and perspectives of farmers. We begin by reviewing research on farmer understanding of heritability and G×E, two fundamental concepts in selection.

14.5.1 Farmer understanding of heritability and G×E

Heritability (h^2) is a key determinant of genetic response (R) (see Section 14.1.3). One of the main factors that decreases h^2 is environmental variability (σ_E^2). Another important and related element affecting the outcome of selection is G×E. Interpretation of G×E will influence plant breeders' approaches to developing and improving crop varieties and their choices of how many and which varieties will be released across agricultural environments (Cooper and Hammer, 1996). For these two important elements that affect the results of selection, experience as well as goals will influence the knowledge of farmers and plant breeders and how each responds to variations in h^2 and G×E in their crop varieties and growing environments.

In comparative research on farmers' concepts of h^2 , farmers were presented with scenarios about both high and low h^2 traits (Figure 14.4, Table 14.1). The goal was to determine if farmers noted the contribution

of σ_E^2 and σ_G^2 to σ_P^2 , and if they distinguished between high and low h^2 traits in their major crop. The first null hypothesis was that there was no difference in distribution of farmers' responses concerning consistency between parent and progeny phenotypes in a typical, variable environment and in a hypothetical, uniform environment for (i) relatively low h^2 traits, and (ii) relatively high h^2 traits. This hypothesis was rejected for low h^2 traits, but accepted for high h^2 traits (most farmers anticipated no change in phenotype regardless of environment), suggesting farmers see little or no contribution of genotype to σ_P^2 for low h^2 traits, and the opposite for high h^2 traits. The second null hypothesis, that farmers' responses indicate no perception of differences in h^2 for relatively low and high h^2 trait expression in a variable environment, was also rejected, supporting the conclusion that farmers do perceive differences in h^2 of traits. Thus, most farmers distinguish between high and low h^2 traits, and consciously select for the former, while often considering it not worthwhile or even possible to seek $R > 0$ for the latter, especially in cross-pollinated crops (Soleri *et al.*, 2002). Given farmers' experiences and the tools and methods available to them, the role of σ_G^2 in low heritability traits is obscured by the σ_E^2 in their growing environments. Similarly, Ceccarelli (1996) argues that plant breeders' lack of experience with growing environments as stressful and variable as those of farmers has obscured plant breeders' ability to perceive qualitative G×E in some MVs between farmers' environments and the more favourable ones they are accustomed to.

To understand farmers' perceptions of spatial G×E interactions we used a scenario with two genotypes originating in contrasting growing environments at three

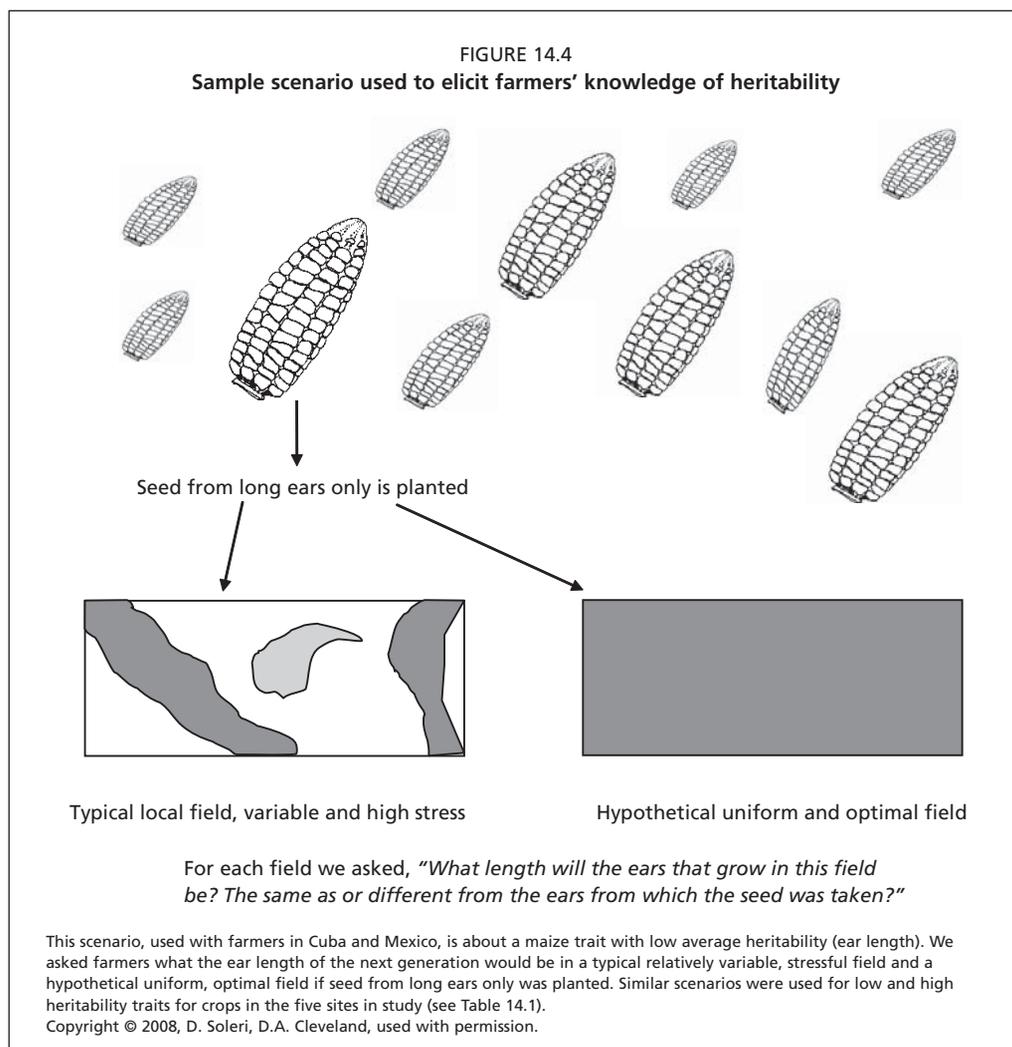


TABLE 14.1

Understanding farmers' perceptions of heritability

Location, crop	Null hypothesis #1: For traits with relatively low or those with relatively high h^2 , distribution of farmers' responses is the same whether scenarios depict typical or optimal environments, i.e. farmers do not see a contribution of environment (Env) to phenotype		Null hypothesis #2: In scenarios depicting a typical environment, distribution of farmers' responses is the same for traits with relatively low or those with relatively high h^2 , i.e. farmers do not see a difference in h^2 between traits
	(a) Low h^2 trait across typical and optimal Envs	(b) High h^2 trait across typical and optimal Envs	Low v high h^2 traits in typical, variable Env
Cuba, maize	Ear length*	Husk colour	Ear length v. husk colour*
Mexico, maize	Ear length*	Tassel colour	Ear length v. tassel colour*
Mali, sorghum	Panicle weight*	Glume colour*	Panicle weight v. glume colour*
Syria, barley	Plant height*	Seed colour	Plant height v. seed colour*
Nepal, rice	Plant height*	Seed colour	Plant height v. seed colour*

* Hypothesis rejected, Fisher's exact test, $P < 0.05$ Based on Soleri *et al.*, n.d.

levels: between locations, between fields in one location, and between places in one field (Soleri *et al.*, n.d., 2002). The results indicated that farmers ($n = 208$) perceive inter- (57 percent) and intra- (30 percent) location $G \times E$ for their major crop, though far fewer at the latter level. $G \times E$ within a field (18 percent) was noted mostly, though not exclusively, by those growing self-pollinated crops, and especially those working at a small scale with intimate knowledge of within-field soil and moisture variations (e.g. rice farmers in western Nepal). Similarly, 37 percent of farmers responded that a qualitative $G \times E$ interaction could occur in their crop due to temporal environmental variation in the form of annual precipitation. In the presence of qualitative $G \times E$, perceptions of the best genetic strategy may differ and be informative about the needs of particular groups or regions. As mentioned in Section 14.4.1 above, farmers tended to favour yield stability over high yield when choosing among varieties in the face of qualitative temporal $G \times E$. This choice was significantly more frequent among farmers in more difficult environments compared with more favourable environments.

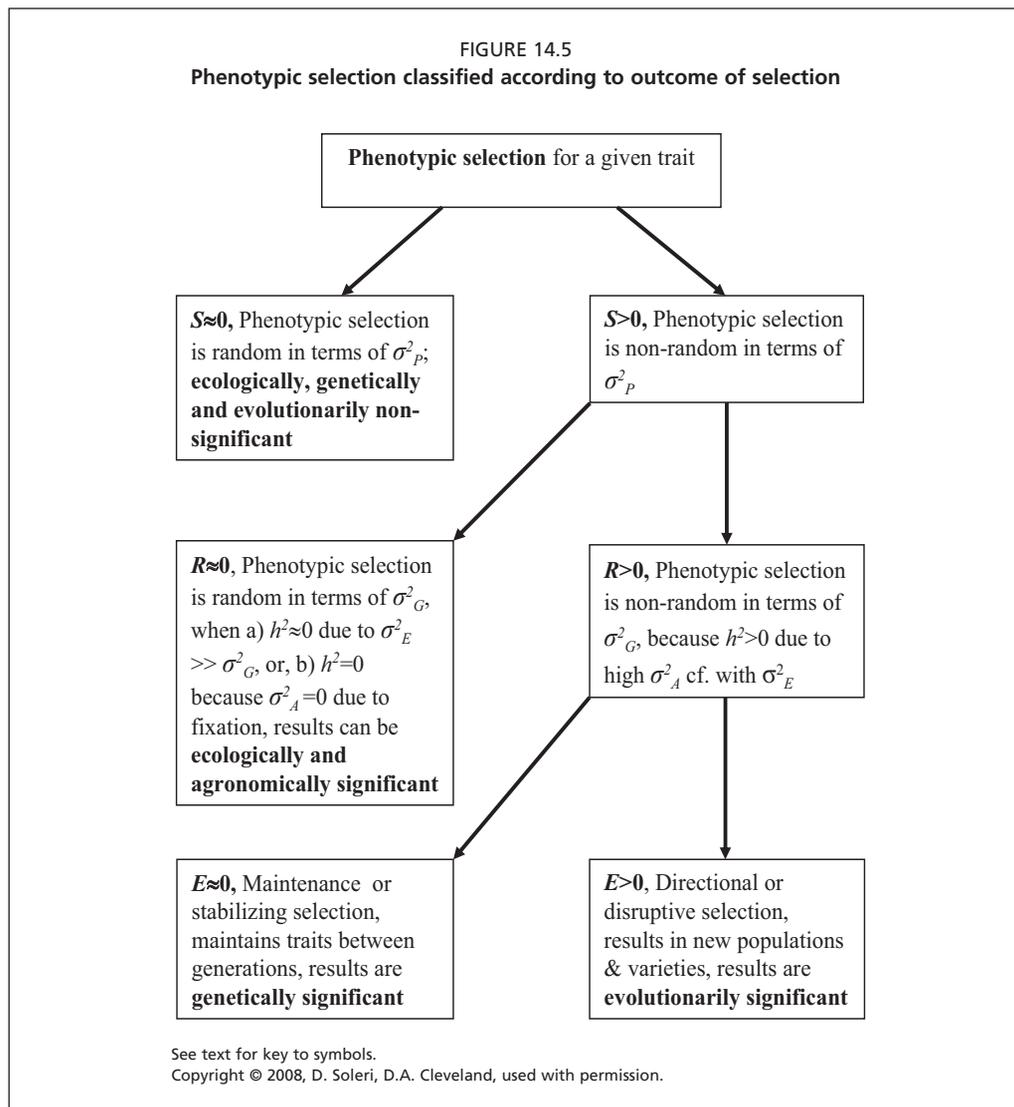
14.5.2 Farmers' selection goals

If plant breeders misunderstand what farmers are and are not attempting to accomplish with their selection practices, it can limit the potential for meaningful collaboration and lead to inappropriate investments of scarce time and resources. Such misunderstandings have grown out of the historical process of separation of farmers' and plant breeders' work (Cleveland and Soleri, 2007).

Just as early evolutionary biologists looked to breeders for empirical demonstration of results of selection that illuminated

evolution, breeders looked to farmers for their applied knowledge and practice that produced practical results in the form of new varieties, as in the early commercial development of maize in the United States of America (Wallace and Brown, 1988: 87–90). With the increased importance of formal science in plant breeding compared with empirical heuristics, and later as plant breeding moved from the public to the private sector (Kloppenburger, 1988), plant breeders began to eliminate farmers from their work (e.g. Schneider, 2002). Plant breeders' and farmers' practices and concepts subsequently developed independently of each other, effectively separating the formal and informal systems of crop improvement and seed multiplication, with plant breeders coming to dominate: "a trend that has been at least locally apparent for 200 years" (Simmonds and Smartt, 1999: 13). Plant breeders focused on modern varieties widely adapted to more optimal, more intensively managed environments, while many traditionally-based farmers in relatively marginal environments continued to focus on traditional, specifically adapted varieties for their diverse, more marginal growing environments (Ceccarelli and Grando, 2002; Cleveland, 2001). When contemporary plant breeders involve farmers in their work, it has generally been limited to the stage of evaluating the plant breeders' populations or varieties in the field (Duvick, 2002), i.e. choosing among different populations or varieties, not selecting among different plants to genetically change existing populations or varieties.

Today, many modern plant breeders consider themselves to be 'applied evolutionists', whose goal is to develop plant varieties better adapted to improved growing environments, with adaptation measured primarily as increased yield



(Allard, 1999: 49). Their emphasis in selection is on achieving directional, multi-generational, micro-evolutionary change. This makes sense given the organization of industrial agricultural systems (see Section 14.2.1 above, and Figure 14.3). It also means that plant breeders often view farmers' selection of seeds or other propagules for planting as a form of mass selection for heritable traits, the process that is assumed to account for crop domestication and for

the ensuing proliferation of crop varieties. It also means formal plant breeders tend to judge the efficacy of farmer seed saving in terms of applied evolution, i.e. the same criteria they apply to their own work, and assume that farmers use these criteria as well.

In the following sections we describe phenotypic selection by farmers organized in terms of possible outcomes: longer-term (multi-generational) genetic change

or micro-evolution (E) [hereafter referred to as 'evolution', in the sense of multi-generational change in the context of agricultural crops, not in the larger biological sense of speciation]; inter-generational genetic change or response (R); and within-generation phenotypic differentiation (S, selection differential) (see Section 14.1.2 above, and Figure 14.1). Where possible, we also discuss farmer goals for selection, although many studies of farmer selection that document genetic or agronomic effects do not document farmers' goals (and vice versa). Note that, regardless of goals, the outcomes of farmer selection can be varied, as depicted in Figure 14.5.

14.5.3 Selection for evolution

The clearest evidence for contemporary farmer selection for evolution is in species that are normally propagated clonally. Some Andean potato farmers search their fields for volunteer seedlings resulting from spontaneous hybridization as a way to diversify their production (Zimmerer, 1996: 201). For example, indigenous South American farmers intentionally incorporate cassava seedlings into recognized varieties, resulting in increased heterogeneity within varieties (Elias *et al.*, 2001; Pujol, David and McKey, 2005). Farmers also select the largest volunteer seedlings, which results in increased heterozygosity as a result of the most heterozygous plants also being the largest, and therefore the least likely to be eliminated during early weeding, although farmers' goals for this selection are unclear (Pujol, David and McKey, 2005).

In seed-propagated species that are predominantly self-pollinated, compared with cross-pollinated species, it is relatively easy to make and maintain evolutionary changes by selecting from among the segregating F_1 plants or those

of later generations, resulting from limited spontaneous cross-pollination. Experimental evidence from Syria shows that farmers could efficiently select among over 200 barley entries (fixed lines and segregating populations), with results in terms of yield potential that equalled, and in one case exceeded, selections by plant breeders in the same environments (Ceccarelli *et al.*, 2000). These findings indicate that farmers have developed selection criteria for identifying high yielding phenotypes that are just as effective as those used by breeders, and more effective in the growing environments typical of those farmers' own fields (Ceccarelli and Grando, 2007).

It is much more difficult to effect evolutionary change in predominantly cross-pollinated, seed-propagated species, especially for quantitative traits with low heritability. However, as described earlier, farmers can discriminate between low and high heritability traits, and use this as a basis for decisions about selection (Soleri *et al.*, 2002). Farmers in Oaxaca, Mexico, often select maize seed with the goal of changing or creating populations with preferred, highly heritable traits, like kernel, tassel and husk colours for culinary and aesthetic reasons (e.g. maize varieties selected for the beauty of their purple tassels) (Soleri and Cleveland, 2001), while the majority of these same farmers see no possibility of changing the key trait of yield, which has low heritability, as discussed below (Soleri and Cleveland, 2001). There is evidence that farmers in central Mexico have selected for and maintained a new landrace, based on seed and ear morphology, among segregating populations resulting from the hybridization of two existing landraces (Perales, Brush and Qualset, 2003). In Rajasthan, India, there is evidence based on research with pearl millet that farmers use

mass selection for low heritability traits in cross-pollinating species with the goal of making directional change in their varieties (Christinck, 2002: 126; Vom Brocke *et al.*, 2002). This research also documented farmers' intentional introgression of modern with traditional varieties of pearl millet, and subsequent selection, resulting in increased genetic variation and long-term directional change (*E*) in selected traits, such as growing period (Christinck, 2002: 123; vom Brocke *et al.*, 2003a).

However, although it is clear that farmers can understand the principle of phenotypic selection and use it to achieve goals of evolutionary change with different crops, this may not always, or even usually, be their goal, or the result.

14.5.4 Selection for genetic response, but not evolution

Farmers also select with the goal of eliminating changes in phenotypic traits resulting from gene flow or natural or indirect phenotypic selection, i.e. to achieve *R* but not *E*. Best documented are farmers' attempts to maintain varietal ideotypes based on quantitative or qualitative phenotypic traits over time in the face of gene flow (Berthaud *et al.*, 2001). Plant breeders can control unwanted gene flow much more effectively in their experimental plots than farmers can in their fields, and in industrial agriculture farmers often buy new seed every year, especially for cross-pollinated crops like maize, eliminating most concerns regarding gene flow.

This type of farmer selection to eliminate changes may contrast with maintenance (stabilizing) selection by plant breeders, which usually has the goal of maintaining yield in the face of changing environments by incorporating new alleles or changing allele frequencies, and may

result in new varieties (i.e. the goal is *E*) (Evans, 1993: 313–314). Like plant breeders (Cooper, Spillane and Hodgkin, 2001), farmers also encourage gene flow under some conditions, for example mixing seed from different sources, planting different populations contiguously or in same plot, and by making crosses, as a way of increasing the variation on which to select.

Farmers can be successful in maintaining varietal ideotypes through direct, intentional selection for key traits, especially for highly heritable phenotypic traits, like those that define a variety. This type of selection is probably most important for cross-pollinated crops, such as pearl millet and maize, as discussed below, since it is much more difficult to maintain populations in these compared with clonally propagated and self-pollinated crops. In eastern Rajasthan, India, amplified fragment length polymorphism (AFLP) analysis showed that farmers maintained the ideotypes of distinct introduced pearl millet FVs, even though they have the same name as local FVs, via intentional selection of panicles for their unique phenotypes (vom Brocke *et al.*, 2003b). In contrast, farmers in Jalisco, Mexico, regularly mix maize varieties together by classifying seed obtained from diverse sources as the same variety based on ear or kernel morphology and colour, which, together with planting patterns, leads to a 1–2 percent level of gene flow between maize varieties during one crop cycle (Louette, Charrier and Berthaud, 1997). A controlled experiment found that, compared with random selection, farmer selection diminished the impact of gene flow on one FV from contrasting FVs for key varietal traits (kernel rows per ear, kernel width and kernel colour), but did not have any effect on allelic frequencies at 9 polymorphic loci coding for traits invisible or unimportant to

farmers (Louette and Smale, 2000). Farmers stated that they were not interested in changing their varieties, but in maintaining varietal ideotypes, and appeared to be achieving their goal. Research in Oaxaca, Mexico, using microsatellite data supported this finding in terms of the results of farmer selection, although farmers' goals were not investigated. Extensive gene flow and little molecular genetic structure was observed, but the maintenance of significantly different maize populations based on morphophenological traits of interest to farmers persisted (Pressoir and Berthaud, 2004b).

A study in Chiapas, Mexico, found that cultural diversity, as measured by ethnolinguistic groups, was not reflected in maize diversity as measured by isozyme variation, but was reflected in some morphological traits (Perales, Benz and Brush, 2005). The differences observed may have been due to unidentified culturally-based networks or practices that structured these maize populations based on farmer selection for a few critical traits against a background of ongoing gene flow (Perales, Benz and Brush, 2005), as was found in the study in the central valleys of Oaxaca, Mexico, (Pressoir and Berthaud, 2004b), although neither study investigated farmer goals in detail.

14.5.5 Selection for intra-generation phenotypic difference

Although farmers are capable of phenotypic selection that is effective in achieving goals of evolution and genetic response, perhaps the most common goal of farmer selection is not genetic, but solely phenotypic, because most of the time a farmer's primary goal in selecting seed is to obtain good planting material. This often means selection for large, clean, disease-free seeds

or other propagules for cross-pollinated (e.g. in maize; Soleri and Smith, 2002), self-pollinated (e.g. in barley; Ceccarelli *et al.*, 2000) and vegetatively propagated crops (e.g. in potato; Zimmerer, 1996). Selection with this goal is also conducted as part of MV seed multiplication (Simmonds and Smartt, 1999: 215). Plant breeders may also carry out this type of selection, for example by removing small seed, but they do this to decrease the contribution of σ_E^2 to σ_P^2 , and so increase heritability with the goal of E .

Research on non-heritable phenotypic differences shows these can have important intra-generational effects in terms of ecology and agronomy. Even in species with high heritability for seed polymorphisms, environment may be an important determinant of seed size and shape, and seed polymorphism can be a significant determinant of differential survival via influence on survivorship and adult plant size (Baskin and Baskin, 2001: 208–214). In maize, for example, larger seed size was found to provide significant advantages in the early stages of plant growth (from germination until stem elongation) (Bockstaller and Girardin, 1994), and was correlated with better early vigour, greater leaf area throughout the life cycle and more rapid development from time of emergence to flowering (Pommel, 1990; Revilla *et al.*, 1999).

When the goal of selection is intra-generational phenotypic differentiation, the result may not be genetic response or evolution, especially for low-heritability traits in cross-pollinated crops. This hypothesis was supported by results of maize seed selection exercises with farmers in two communities in Oaxaca, Mexico. The exercises were done with maize ears post-harvest, which is the way these farmers and most others in Mexico select maize seed. Their selections resulted in high S

TABLE 14.2

Farmers' expectations for response to selection for their primary selection criterion in the major crop they grow

Country, crop, trait (n)	Question A. Farmers responding that response to intentional selection for 10 cycles > random selection for 10 cycles ($IS_{10} > RS_{10}$)				Question B. For farmers responding $IS_{10} > RS_{10}$ to Question A, those stating that response to intentional selection for 11 cycles > random selection for 10 cycles + intentional for 1 cycle ($IS_{11} > RS_{10} + IS_1$)			
	n	%		P	n	%		P
Mexico, maize, ear length (59)	23	39	*	0.000000	6	26	*	0.000000
Cuba, maize, ear length (29)	27	93		0.245614	12	44	*	0.000002
Syria, barley, plant height (21)	20	95		0.499999	11	55	*	0.000614
Nepal, rice, grain yield (40)	39	98		0.499999	17	44	*	0.000000
Mali, sorghum, grain yield (40)	35	88		0.057662	23	66	*	0.000078
Total (189)	144	76	*	0.000000	69	48	*	0.000000

One sided Fishers' exact test, of the null hypothesis that, similar to plant breeders, farmers would see intentional selection as achieving a greater response compared to random selection. Calculated using SISA (<http://home.clara.net/sisa/>). RS = random phenotypic selection by farmer, IS = intentional phenotypic selection by farmer.

Based on Soleri *et al.*, n.d.

Some farmers said large seed resulted in higher germination, larger seedlings, early vigour and higher yields, although most farmers attributed their preference for large seed to 'custom'.

It is still possible that simple mass selection for intra-generational phenotypic differences could result in *R* or *E* even if these are not farmer goals. As mentioned above, it is not clear what importance this had during domestication and subsequent diversification of crops, versus intentional selection for short-term change or long-term maintenance. For example, maize farmers in Uganda and the United Republic of Tanzania, like those in Mexico, were reported to select for large, clean kernels from large ears, apparently because they believed that these germinated well and produced high-yielding plants (Gibson *et al.*, 2005). Interestingly, this appeared to result in decreased resistance to maize streak virus, since resistant plants had smaller ears, and plants with large ears appeared to be non-resistant escapes.

As part of a comparative five-country study of FK and PBK (Soleri *et al.*, 2002, 2004), farmers were presented with

a hypothetical scenario asking them to compare random with intentional selection for 10 cycles in a typical field, in populations with phenotypic variation for the trait they used as major selection criterion (Figure 14.6) (Table 14.2, question A). The null hypothesis was that farmers did not differ from plant breeders, i.e. that they would all consider intentional selection to be more effective than random selection for improving or at least maintaining this trait. The majority of responses corresponded to the null hypothesis of no difference between farmer and plant breeder expectations that intentional selection was more effective for increasing yield, 76.2 percent (144/189), although those who disagreed with that idea were sufficient to reject the hypothesis statistically ($P = 0.00000$). Disagreement was particularly frequent among maize farmers, probably due to recombination in that cross-pollinating crop.

These results indicate that farmers who believe there is an advantage of intentional over random selection, see their goal for phenotypic selection as either *S* or *R* or *E*. To discriminate between these possibilities, and with the same null hypothesis as

outlined above, those farmers responding to the first question that intentional selection resulted in greater yield, were asked to compare random selection for 10 cycles followed by one cycle of intentional selection, with 11 consecutive cycles of intentional selection. Results differed significantly from the null hypothesis (Table 14.2, question B). Among these farmers, only 23.2 percent (20/86) saw 11 years of intentional selection as superior. These results demonstrate that among those farmers favouring intentional selection, only a minority see it as providing cumulative multi-generational change (*E*), while the primary selection goal of the other farmers who saw an advantage to multi-generational intentional selection for low-heritability yield-related traits is either eliminating changes between generations (*R*) or a non-genetic advantage they believe is fully achieved within one year (*S*). The large number of farmers who do not consciously see an advantage to multi-generational intentional selection, but who, like other farmers, select for large seed from large, clean ears, may do so because of custom, as did the majority of farmers in the selection experiment described earlier.

14.6 CONCLUSIONS

Many elements of crop variety choice and plant selection in the Third World contrast substantially with industrial agricultural systems, including the growing environments, genetic resources and organization of the agricultural system. The urgency of understanding farmer selection will increase in the future with global climate changes, the continuing loss of genetic resources, the rapid spread of transgenic crop varieties, the development of a global system of IPR in crop genetic resources, the need to make agriculture more sustainable while feeding more people,

and the movement to make formal plant breeding more relevant to farmers through PPB. Understanding farmers' choice and selection practices, their biological results, the knowledge and goals underlying them, and the similarities and differences with plant breeders provides a means for the two groups to work together more effectively. This understanding and collaboration is critical for supporting all of the important functions of SSTW agriculture, including long-term global food security.

For PPB, this means that farmers' goals for varietal choice and phenotypic selection need to be understood in the context of a system that integrates production, consumption, improvement, multiplication and conservation. The biological result of phenotypic selection needs to be evaluated in terms of its possible ecological effects (via *S*), as well as in terms of *R* and *E*. Additionally, farmers' theoretical knowledge of choice and selection, not just their criteria, need to be understood by plant breeders to fully realize the potential benefits of collaboration. The value of this research will be judged by its effectiveness in improving the efficiency and outcomes of collaborative breeding by scientists and farmers, and improvement in the well-being of those farmers and their communities.

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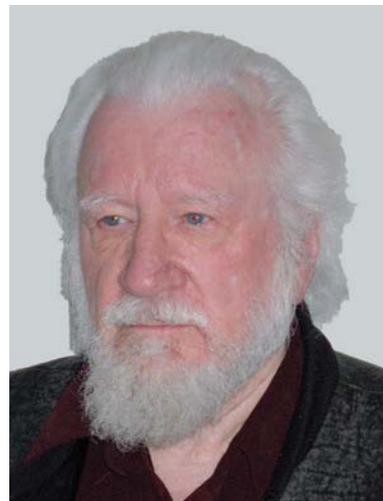
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CHAPTER 15

Breeding for quantitative variables

Part 2: Breeding for durable resistance to crop pests and diseases

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15.1 INTRODUCTION

There are three categories of plant breeder. First is the professional, who is a highly trained scientist with a profound knowledge of modern genetics and related subjects. Second is the amateur, who uses simple selection techniques to produce new varieties. Third is the subconscious selector who unwittingly changes plants by artificial selection. It is these subconscious selectors who were responsible for all the original domestication of plants, and for much of the modern artificial selection in Third World countries.

There were no professional plant breeders before 1900, and all plant breeding was done by amateurs and subconscious selectors. The classic example of an amateur was a farmer called Rimpau who, in 1866, started selecting the best rye plants in his crop for use as seed. He did this with each successive crop and, after twenty years, he had a greatly superior rye known as 'Schlanstedt', which quickly became popular in much of Europe. In this chapter, participatory plant breeding is taken to mean cooperation between professional and amateur plant breeders.

During the twentieth century, there were major changes. Between 1900 and 1905, three seminal discoveries were made. These were the recognition of Mendel's laws of inheritance, Johannsen's discovery of pure lines, and Biffin's discovery of single-gene resistances. All subsequent plant breeding was done by scientific professionals, who were totally captivated by these new discoveries. Amateur plant breeders disappeared almost entirely. More recently, the techniques of genetic engineering have become popular, but these, of necessity, involve single-gene resistances, and they usually require professional scientists.

The switch from amateur to professional breeding occurred because there are two kinds of breeding, depending on whether the breeding is for multiple-gene or single-gene characters. Rimpau was working with multiple-gene characters, and he obtained small, quantitative improvements with each generation of selection. However, when it came to resistance to crop pests and diseases, the professional breeders were working with single-gene resistances, because they had a choice and they chose this method as it gives a quick response. This single-gene breeding is usually too complex and too difficult for amateur breeders, and this was why they disappeared during the twentieth century.

Today, the pendulum is swinging back again, and there is a new appreciation of the value of both amateur breeders and multiple-gene resistances. Participatory plant breeding, using multiple-gene resistances, now provides an admirable opportunity for cooperation between amateurs and professionals.

15.1.1 Crop parasites

In this chapter, a crop parasite is defined as any organism that spends a major part of its life cycle inhabiting one host individual, and obtaining nutrients from that host. The host, of course, is a crop plant. A parasite may be an insect, mite, nematode, parasitic angiosperm (e.g. broomrape, witchweed, dodder), or any of the various categories of plant pathogen, such as fungi, bacteria and viruses. However, weeds are not parasites: they are competitors, and they are not part of this discussion.

This chapter is addressed to both participating, amateur plant breeders, who may find *Return to Resistance* (Robinson, 1996) helpful, and to cooperating professional breeders who may find *Self-Organising Agro-Ecosystems* (Robinson, 2004) useful.

15.1.2 Plant breeding

For the whole of the twentieth century, scientific plant breeding has had four main objectives. These were improvements in (i) yield; (ii) quality of crop product; (iii) agronomic suitability; and (iv) resistance to parasites. This scientific breeding has been remarkably successful in the first three of these objectives, but much less successful with breeding for resistance. The basic reason for this has been that resistance kept breaking down because of new strains of the parasite. There was then an apparently endless repetition of resistance failures and a 'boom and bust' cycle of cultivar production.

Vanderplank (1963, 1968) first made a clear distinction between single-gene and multiple-gene resistances to crop parasites. He called single-gene resistance 'vertical resistance', and it is normally qualitative in that it provides complete protection or none at all, with no intermediates. He called multiple-gene (polygenic) resistance 'horizontal resistance', and it is quantitative in that it can provide every degree of protection from a minimum to a maximum.

15.1.3 Stability and instability

Any protection mechanism against a crop parasite may be described as unstable or stable. An unstable resistance is *within* the capacity for micro-evolutionary change of the parasite. This means that the parasite is able to produce a new strain that is unaffected by that protection, which is then said to have 'broken down' (strictly speaking, the protection is unaltered, and it is the parasite that has changed). Many synthetic insecticides and fungicides provide unstable protection, and they sooner or later break down in the face of new strains of the parasite. Single-gene, vertical resistances are almost always unstable, and they too

break down as new races, strains, biotypes or pathotypes of the parasite emerge.

Horizontal resistances provide stable protection. That is, they are *beyond* the capacity for micro-evolutionary change of the parasite, which is consequently unable to produce a new strain that is unaffected by that resistance. Other protection mechanisms can also be stable. Examples of stable insecticides include natural pyrethrins, rotenone, and a film of oil on water to control mosquito larvae. Examples of stable fungicides include both copper and dithiocarbamate formulations.

15.1.4 Vertical resistance

Vertical resistance has several remarkable advantages. First, it provides complete protection against a parasite. There are a few examples of incomplete vertical resistance (see below) but not enough to invalidate this rule. Second, it usually has a very wide climatic range and can be employed across broad geographical regions. Third, being controlled by single genes, it is amenable to gene-transfer and back-crossing techniques. These techniques are so elegant, and so beautiful, that they were greatly favoured by professional breeders during the twentieth century.

However, vertical resistance does have some grave disadvantages. First, as already mentioned, it is unstable. It is liable to break down when faced by new strains of the parasite. The speed of this breakdown can vary greatly. The fastest occurs in the first growing season, and this happened with *Puccinia polysora* of maize in tropical Africa (see below), and in Late potato blight (*Phytophthora infestans*) in the Toluca Valley of Mexico, which is the centre of origin of this fungus. The slowest breakdowns take so long to occur that the vertical resistance is effectively durable (see

below), but these are too rare to be a general breeding tool.

A second disadvantage of vertical resistance is that it is responsible for the vertifolia effect, which is the gradual loss of horizontal resistance during breeding for vertical resistance, and which is described in more detail below. A third disadvantage is that vertical resistances occur only against some species of parasite. Consequently, it is not possible to use vertical resistance for all the locally important parasites.

In general, vertical resistance is not recommended for participatory plant breeding. This is mainly because the failure of a wonderful new cultivar, which has taken years of devoted work to produce, by both professional and amateur breeders, is quite frankly heart-breaking. Nothing can be expected to discourage amateur breeders more than this. An essential aspect of participatory plant breeding is that we maintain the confidence of the participating amateurs. Consequently, participating professional breeders should be very cautious about recommending the use of vertical resistance, or even the combined use of vertical and horizontal resistance, in participatory plant breeding.

15.1.5 Horizontal resistance

Being a quantitative variable, horizontal resistance can be expressed at any level between a minimum and a maximum. In the absence of crop protection chemicals, the minimum level of horizontal resistance usually results in a total loss of crop from the parasites. And the maximum level of horizontal resistance usually results in negligible loss of crop. However, the maximum level of horizontal resistance never provides as complete a protection as vertical resistance. Even with the highest level of horizontal resistance, there is always some slight parasitism.

The main advantage of horizontal resistance is that it is durable, and that it is possible to breed for increased levels of many different quantitative variables simultaneously. Participatory plant breeders can accordingly aim at high levels of horizontal resistance to all locally important parasites. This will achieve crop husbandry that is effectively free of all parasite damage, and one that is free of pesticides as well. And these freedoms will be permanent. However, it must be emphasized that this is the objective. Such an objective may prove impossible to achieve in practice, at least in some crops, and in some areas. But, even if this objective is unattainable, there will be at least some improvement over current farming practices in terms of increased yields and decreased damage from parasites.

15.1.6 Two kinds of plant breeding

Clearly, the key difference in breeding crop plants for temporary and durable resistances is the difference between breeding for single-gene and multiple-gene characters.

Breeding for single-gene characters requires both pedigree breeding and backcrossing, or the very modern techniques of marker assisted selection and genetic engineering. Anyone using these techniques for acquiring resistance should assume that the resulting resistance will be unstable, and that it will have a very high probability of breaking down sooner or later.

Breeding for multiple-gene characters, such as horizontal resistance, requires an entirely different breeding technique, called recurrent mass selection, which is discussed below.

15.2 WHY WAS TEMPORARY RESISTANCE SO POPULAR?

During most of the twentieth century, vertical resistance was consistently the resist-

ance of choice, and horizontal resistance was almost entirely ignored. This is a historical fact, and it is so important that we must examine its causes in some detail.

The effectiveness of horizontal resistance is influenced by many quantitative variables. Many of these variables are difficult to observe or measure, and there is a powerful tendency to neglect them. Twentieth-century plant breeders did neglect them, and this is why they also neglected horizontal resistance. They concentrated on vertical resistance because it is complete. This completeness was very attractive. It meant that the parasite control was total. However, the ephemeral nature of the resistance was usually revealed only much later.

Today, if we are to breed crops successfully for resistance that is durable, we must understand these misleading, quantitative variables that disguise the effectiveness of horizontal resistance. Within the framework of participatory plant breeding, a primary function of the participating specialists must be to ensure that the participating farmers are not deceived by these misleading variables.

15.3 MISLEADING VARIABLES

In principle, breeding for horizontal resistance is very simple and very easy and for this reason it is ideal for participatory plant breeding. But there are a number of factors that can be horribly misleading and which, unless understood, can lead to totally false observations. These false observations often disguise horizontal resistance so effectively that little genetic advance can be seen.

It was these sources of error that led to vertical resistance being the preferred resistance mode among plant breeders for the whole of the twentieth century. Being qualitative, vertical resistance is easily seen, but its unstable nature is not apparent.

Being quantitative, in contrast, horizontal resistance is easily obscured, its durability not recognized, and its value consistently underestimated. A clear comprehension of these misleading variables, these sources of error, is consequently essential for anyone wishing to breed crops for durable resistance. The twelve most important of them are considered below. They are summarized in Table 15.1.

15.3.1 Parasite interference

The only way to measure the level of horizontal resistance is by the level of parasitism. Parasite interference can make such assessments wildly inaccurate, and the level of parasitism is then a thoroughly misleading indication of the level of horizontal resistance. Parasite interference occurs because the parasites are mobile, and they can move from plot to plot, or from plant to plant. The importance of this phenomenon was first discovered by Vanderplank (1963).

Parasite interference can be seen with field trials in which the parasites can move from one plot to another. The results of parasite interference can be extraordinary, and may lead to errors of several hundred-fold (James *et al.*, 1973). In these circumstances, the effects of horizontal resistance can be totally obscured. Parasite interference is at its worst in the very small screening plots produced by the technique of 'ear-to-row' selection (or family selection), often used during the breeding of self-pollinating small-grain cereals and pulses. The parasite interference can be so intense that plants with a functioning vertical resistance can appear diseased, because of millions of hypersensitive flecks produced by the failed infections of non-matching strains of the parasite. Imagine the level of parasitism, therefore, if those infections are produced

TABLE 15.1
Summary of misleading variables

Misleading Variable	Problem	Solution
Parasite interference	Hides high levels of horizontal resistance	Use relative measurements only
Epidemiological competence	Resistance requirements vary between agro-ecosystems	Use on-site screening
Environmental erosion	An apparent loss of horizontal resistance due to re-location in an area of higher epidemiological competence	Each agro-ecosystem should have its own breeding programmes
Vertifolia effect	The loss of horizontal resistance when breeding crops for vertical resistance, or under the protection of crop protection chemicals	Inactivate all vertical resistances, and avoid any use of crop protection chemicals
Parasite erosion	An apparent loss of horizontal resistance due to changes in the parasite population	Screen in an area of high parasite density
False erosion	An apparent loss of horizontal resistance due to sloppy or negligent assessments	Be more careful
Biological anarchy	An increased epidemiological competence in the parasite due to the loss or debilitation of biological control agents	This phenomenon will disappear after a few seasons of freedom from pesticides, as the biological controls are restored by the use of horizontal resistance
Population immunity	Makes field assessments preferable	Avoid laboratory assessments of resistance
Chance escape	Provides a false indication of resistance	Inoculate the screening population, or use grid screening
Quantitative vertical resistance	Looks like horizontal resistance but is not	Use parents that lack vertical resistance genes, or use the one-pathotype technique (see below).
Durable vertical resistance	This rare phenomenon provides a false hope for breeders of single-gene resistances	Do not rely on this remote possibility
Sub-optimization	Do not breed for a single resistance mechanism, or resistance to single species of parasite	Use the holistic approach (see below)

by a matching strain, against which the vertical resistance does not operate.

Parasite interference can also occur among individual host plants. Consider a screening population in which there are wide differences in horizontal resistance between individual plants. A quantitatively resistant plant may be surrounded by susceptible plants. The overcrowded parasites will then move onto that resistant plant, making it look far more susceptible than it really is. Once again, the magnitude of these errors can be great. In fact, if that resistant plant were growing in a farmer's field, as a pure line or clone, there would be no parasite interference, and its resistance might then be entirely adequate to provide complete control of the parasite.

The misleading effects of parasite interference can be avoided during breeding for horizontal resistance by using *relative* measurements during screening. That is, the *least parasitized* individuals are selected regardless of how severely parasitized they might be. In the early breeding cycles, these least-parasitized individuals may well look so awful that the breeder could be forgiven for concluding that there is no point in continuing. But that would be a mistake. However awful they may look, they are the least susceptible individuals of an early breeding cycle and, as such, they should become the parents of the next breeding cycle.

Remember also that we are breeding for comprehensive horizontal resistance

to all the locally important parasites. This requires the one quality of 'good health'. The least parasitized individuals will be fairly susceptible to many different species of parasite. Their quality of 'good health' will be low. But it will be higher than all those other, less healthy individuals in the screening population, many of which may have disappeared entirely.

A final comment about parasite interference concerns the movement of parasites from one farm, or one district, to another. Many organic farmers are able to cultivate fairly susceptible cultivars successfully because their neighbours are using crop protection chemicals. The district interference is then minimal. But were all the farmers in that district to eschew crop protection chemicals, the parasite populations would be so large, and the district interference so great, that the use of those cultivars for organic agriculture might prove impossible. The other side of this coin is that progress in breeding for horizontal resistance will lead to reductions in district interference, which, in turn, will enhance the effects of that horizontal resistance.

15.3.2 Epidemiological Competence

Epidemiological competence refers to the ability of a crop parasite to cause an epidemic (or infestation). It is another biological variable that can be expressed at any level between a minimum and a maximum.

Consider a wild ecosystem, which might, perhaps, extend up a mountainside. The epidemiological competence of a plant parasite might change along a gradient from low to high moisture, or temperature, or whatever factor is governing that epidemiological competence within the ecosystem. The various host ecotypes along that gradient will have corresponding levels of horizontal resistance. Where the

epidemiological competence is low, the horizontal resistance will also be low, because there is little selection pressure for resistance. But where the epidemiological competence is high, the level of horizontal resistance will also be high, because there is strong selection pressure for resistance.

When breeding for horizontal resistance, this variation in epidemiological competence is important in two ways. First, we must use 'on-site screening'. This means that the screening for horizontal resistance must be conducted: (i) in the locality of future cultivation; (ii) in the time of year of future cultivation; (iii) in the field (i.e. not in the laboratory or greenhouse); and (iv) according to the farming system (e.g. organic or conventional, irrigated or rainfed) of future cultivation. On-site screening is particularly well suited to participatory plant breeding.

Second, each distinct agro-ecosystem will require its own horizontal resistance breeding programme for each of its crop species. This programme must be aimed at the levels of epidemiological competence of the locally important parasites. In practice, this is not difficult. Agro-ecosystems are usually quite large, and the necessary levels of horizontal resistance will be discovered by practical farming experience, spread over time, as the breeding programmes produce more and more new cultivars, with higher and higher levels of comprehensive horizontal resistance.

15.3.3 Environmental erosion of horizontal resistance

If a cultivar has adequate horizontal resistance in an agro-ecosystem in which the parasite has a relatively low epidemiological competence, and that cultivar is taken to a different agro-ecosystem, where the parasite has a high epidemiological competence, the

resistance will appear to have decreased, possibly disastrously. This is known as environmental erosion of horizontal resistance. Strictly speaking, of course, the resistance is unchanged and it is the epidemiological competence of the parasite that is different. But the level of parasitism increases and this can be alarming if the cause is not understood.

It is because of these differences in epidemiological competence between agro-ecosystems that we speak of 'locally important parasites'. We are breeding agro-ecotypes (i.e. cultivars) for our own agro-ecosystem. These agro-ecotypes may have too much, or too little, resistance in other agro-ecosystems, where the epidemiological competences are different. But these other agro-ecosystems are not our concern. Equally, other people's agro-ecotypes will very likely prove inferior in our own agro-ecosystem. Professional breeders often speak of site-specific plant breeding in which the breeding targets are aimed at a particular site with special requirements. On-site selection fits in well with this concept.

The environmental erosion of horizontal resistance seems like a breakdown of that resistance but, clearly, it is not.

15.3.4 The vertifolia effect

The vertifolia effect was first recognised by Vanderplank (1963) and it is an erosion of horizontal resistance resulting from genetic changes in the host species which occur during breeding for vertical resistance. These changes can also occur during any breeding that is conducted under the protection of crop protection chemicals.

This erosion occurs because horizontal resistance can be measured only in terms of the level of parasitism. If the level of parasitism is totally obscured by pesticides, or by a functioning vertical resistance, the level of horizontal resistance

cannot be observed or assessed. Because individuals with the highest levels of horizontal resistance are always a minority in a screening population, less-resistant individuals are more likely to be selected on the basis of their other attributes.

After many generations of crop breeding conducted under the protection of pesticides or vertical resistance, or both, the levels of horizontal resistance in modern cultivars are usually low. This erosion of horizontal resistance has continued for about a century in many species of crop. It has been particularly serious in potatoes, tomatoes and cotton, but there are few species in which it has not occurred. It is also the reason why breeding for horizontal resistance is now so important.

The lesson of the vertifolia effect is that we must never protect our screening populations with crop protection chemicals. However, there is one exception to this rule. In the early screening generations, even the least parasitized individuals may be so severely damaged that their very survival is threatened. In such a case it is permissible to use crop protection chemicals as a last resort to preserve the parents of the next generation. Equally, we must never use vertical resistances in our screening populations. Methods of avoiding this are described below.

People who call themselves 'seed savers' know that century-old cultivars, often called 'heirloom varieties', usually have higher levels of durable resistance than modern cultivars. This difference is a measure of the overall vertifolia effect that has occurred during the twentieth century.

15.3.5 Parasite-erosion of horizontal resistance

Occasionally there can be changes in the parasite population that lead to an

increased epidemiological competence. This can happen, for example, with the *Fusarium* and *Verticillium* wilt fungi. The frequency of the highly pathogenic forms of these soil-borne pathogens might be quite low in the area of field screening. However, with repeated use of one field for the screening work, the frequency of pathogenic forms will increase, more or less in step with the increases in horizontal resistance in the host. The overall effect is then an appearance of no progress whatever, with a very real possibility of the breeding programme being abandoned.

This is a somewhat rare phenomenon and the participatory breeder is unlikely to be faced with it very often. However, it is as well to be aware of the possibility, just in case of apparently discouraging progress. As a general rule, however, the parasitic ability of most crop parasites, particularly the obligate parasites, is fixed, and parasite-erosion is rare.

15.3.6 False erosion of horizontal resistance

There can be false erosion of horizontal resistance due to sloppy techniques, or just plain carelessness. The classic example of this occurred with a virus disease of sugar cane called mosaic. This disease can be devastating when susceptible cultivars are being cultivated. However, in most areas, the disease was controlled so completely with horizontal resistance that it tended to be forgotten. New cultivars that were released to farmers were susceptible because they had been inadequately tested, or not tested at all, for resistance to this virus, and there would then be a flare up of the disease. It was not uncommon for this to be blamed on a breakdown of resistance when, of course, it was nothing of the kind.

15.3.7 Biological anarchy

Biological anarchy is the converse of biological control. It means that the various agents of biological control have been depleted or destroyed by crop protection chemicals, particularly when there has been pesticide overload. These agents might be hyper-parasites, predators, microbiological competitors, toxin-producing micro-organisms, or organisms that stimulate resistance responses in the host. The importance of biological anarchy is revealed by the success of integrated pest management, generally known as IPM. This method involves careful monitoring of the crop parasites in order to reduce the use of crop protection chemicals to the absolute minimum necessary for control. A gradual increase in biological control then occurs. When the biological controls are restored, a greatly reduced rate of crop protection chemical application can be maintained.

The importance of biological anarchy during breeding for horizontal resistance is that, in the absence of biological controls, many crop parasites will behave with a savagery that would be impossible if the biological controls were functioning. This means that assessment of the level of horizontal resistance can be difficult. Screening for horizontal resistance should be conducted in an area where there is no biological anarchy. But, given the widespread use of crop protection chemicals, particularly in the industrial nations, it is often impossible to find such an area. The screening population then appears to have so little resistance that grave doubts develop concerning the wisdom of this approach. However, the problem of biological anarchy is less acute in developing countries, where the use of crop protection chemicals is much less intense.

It should be added that the best way to restore biological controls is to use horizontal resistance. And the best way to enhance the effects of horizontal resistance is to restore biological controls. The two effects are mutually reinforcing. The practical effect of this is that a new cultivar with apparently inadequate horizontal resistance may well prove to have adequate horizontal resistance, once the biological controls are restored. This restoration may require several seasons of cultivation without pesticides but, once complete, the effects can be dramatic.

It should also be added that the agents for biological control often depend on a small population of the parasite in order to maintain their own populations. A low level of parasitism is often desirable for this reason, provided that it has no deleterious effect on the yield or quality of the crop product. However, purchasers of organic food often like to see minor parasite damage as evidence for freedom from crop protection chemicals.

15.3.8 Population immunity

Population immunity means that a host population is effectively immune, even though the individuals that make up that population are less than immune. This is because population growth, unlike an individual's growth, can be positive or negative. Positive population growth means that there are more births than deaths, and the population is increasing. Negative population growth means that there are more deaths than births, and the population is decreasing. The dividing line occurs when the births and deaths are equal, and the population growth is then zero.

Now consider a crop parasite. In order to cause an epidemic (or infestation), the parasite population growth must be positive.

Indeed, it must be strongly positive if it is to become a serious crop pest or disease. Each individual parasite must spawn more than one new individual before it dies. Now suppose that the combination of horizontal resistance and biological controls is such that, on average, each parasite individual spawns less than one new individual. The parasite population growth is now negative, even though the host individuals are not immune. This situation is population immunity, and it is important in horizontal resistance breeding in three quite different ways.

First, population immunity means that we do not need to breed for the maximum levels of horizontal resistance. We need to breed for enough horizontal resistance to cause population immunity, and no more. This level is discovered from practical farming experience.

Second, although vertical resistance can be assessed on detached leaves in a test tube, or leaf disks in a Petri dish, or even entire plants in a growth chamber, horizontal resistance should not be measured in this way. This is because these laboratory methods cannot possibly represent the effects of biological controls or population immunity. The levels of horizontal resistance are best determined in the field and, if at all possible, under conditions of restored biological controls. Once again, the best determinations will be the result of practical farming experience.

Third, all measurements and descriptions of horizontal resistance must be relative. There can be no absolute measurements. We can describe a new cultivar "A" as being more resistant to a particular parasite than cultivar "B", but less resistant than cultivar "C". But we cannot have an absolute scale of measurement comparable to the Celsius scale of temperatures. This is because these

biological variables are too imprecise to define accurately. However, this does not make horizontal resistance any less useful in farmers' fields.

15.3.9 Chance escape

The distribution of parasites in a screening population is often uneven. This is called a 'patchy distribution' and it is most common with soil-borne parasites and gregarious insect pests. There may then be some host individuals that have no parasites at all, and they give the impression of being highly resistant. They are known as 'chance escapes' and, obviously, they should not be selected as parents of the next screening generation because they could be very susceptible. But the problem is how do we recognise them, and how do we avoid them? There are a number of techniques that increase the accuracy of the screening, depending on the nature of the parasite. It is in this area that the professionals will be most useful to participatory amateur breeders.

If the parasite is soil-borne, such as a root nematode, or a fungal or bacterial wilt organism, it is a good idea to pre-germinate the seedlings in flats or peat pots for later transplanting in the field. These flats or pots can then be inoculated with the parasites in question, and the very process of transplanting will ensure an even distribution of the parasite.

If the parasite is a gregarious insect, in which all individuals tend to congregate on one host plant, they can often be redistributed on a daily basis by disturbing them. This can be particularly important with virus vectors.

If the parasite is seed-borne, it is usually feasible to inoculate the seed before sowing. The details of the techniques for doing this vary considerably with different kinds

of parasite and, with participatory plant breeding, this will be the responsibility of the professionals.

If the parasite is wind-borne, such as most fungal spores, or a flying insect, a previously prepared population of the parasite can be released, blown or water-sprayed on to the screening population. Once again, the details of the techniques vary and will be handled by the professionals.

With some parasites, inoculation is not feasible for technical reasons. An alternative technique is then to ignore those parts of the screening population that are free of the parasite in question. Or any individual plant that is entirely free of the parasite in question can be ignored. This procedure runs the risk of discarding some highly resistant potential parents, but this wastage is preferable to the risk of selecting highly susceptible escapes as parents of the next generation.

Finally, there may be parasite gradients within the screening population in which the intensity of parasitism changes gradually from low to high from one part of the host population to another. This effect can be eliminated by dividing the screening population into a grid of suitably sized squares. Only the least parasitized individual is selected within each square, regardless of the level of that parasitism when compared with other squares.

15.3.10 Quantitative vertical resistance

Occasionally, vertical resistance can be quantitative and it is then easily confused with horizontal resistance. It occurs, for example, with Hessian fly (*Mayetiola destructor*) of wheat (Dent, 1998). Fortunately, this situation is rare and need not worry the breeders of most crops. However, if it does occur, quantitative vertical resistance must obviously be avoided or inactivated during

breeding for horizontal resistance. This can be done either by using only parents that are known to possess no genes for quantitative vertical resistance. Alternatively, the ‘one-pathotype technique’ (described below) may be employed.

15.3.11 Durable vertical resistance

Very occasionally, single-gene vertical resistances may be durable. This happens, for example, with cabbage yellows (*Fusarium oxysporum* f.sp. *conglutinans*) in the United States of America, potato wart disease (*Synchytrium endobioticum*) in Britain, and wheat stem rust (*Puccinia graminis*) in Canada (Vanderplank, 1978). The durability is usually due to local circumstances that would not occur in the wild pathosystem of the host and parasite progenitors. However, durable vertical resistance can be very useful, and there is no reason why it should not be exploited. But durable vertical resistance is so rare that it should not be aimed at, nor depended on, in most breeding programmes. It led many plant breeders astray in the twentieth century, as they continued to hope, over-optimistically, that their single-gene resistances would also prove to be durable.

A technique that has had some success is the ‘pyramiding’ of single-gene resistances. This involves putting as many different vertical resistance genes as possible into one plant in a so-called ‘pyramid’, and this can prolong the life of vertical resistance, particularly if genes from different species of wild plants are combined. However, this is resistance breeding at its most difficult and is of doubtful value for participatory plant breeders. If it is employed, it will require professional plant breeding at a plant breeding station combined with selection in farmers’ fields.

15.3.12 Sub-optimization

Sub-optimization means emphasizing some subsystems at the expense of others, usually by working at too low a systems level. There are many levels of subsystem in biological systems and sub-optimization can lead to two kinds of error. First, by working at too low a systems level, other subsystems may be overlooked. Second, emergent properties, which can be observed only at their own systems levels, may also be overlooked.

An obvious example of sub-optimization in biology occurs with the ‘schooling’ of fish. This schooling is an emergent property in which a population of fish swim as one individual. A scientist studying only one fish, or even a pair of mating fish, in an aquarium, cannot possibly observe this emergent property of schooling. In order to study schooling, the scientist must work at the higher systems level of the population.

During the twentieth century, plant breeding for resistance to parasites suffered considerably from sub-optimization. Research was conducted at the systems level of the individual host or parasite, or even the individual resistance mechanism. It should also have been conducted at the level of the two interacting populations of host and parasite, which is a systems level now called the *pathosystem*. A pathosystem is a subsystem of an ecosystem and, when host resistance is studied at this level, very different pictures of both vertical resistance and horizontal resistance emerge. This is because of previously unobserved emergent properties.

We now recognize the significance of two different kinds of infection. Infection is defined as *the contact made by one parasite individual with one host individual for purposes of parasitism*. With allo-infection, the parasite has to travel to its host, having

originated somewhere else. This is analogous to cross-pollination, or allogamy. With auto-infection, the parasite is born, hatched or spawned on the host that it is infecting. This is analogous to self-pollination, or autogamy. We also recognize that, in a wild pathosystem, vertical resistance can control allo-infection only, and auto-infection can be controlled only by horizontal resistance (although horizontal resistance can also control allo-infection).

The control of allo-infection by vertical resistance apparently operates as a system of locking, with each host having a biochemical lock, consisting of several resistance genes, and each parasite having a biochemical key consisting of several parasitism genes. If the parasite key does not fit the lock of the host it is allo-infecting, the infection fails, while if the key does fit the lock the infection succeeds. Such a system ensures that the frequency of matching allo-infection is low, and this stabilizes the population explosion of the parasite. This stabilization is an emergent property that can be seen only at the level of the system of locking, the level of the pathosystem.

However, if every door in the town has the same lock, and every householder has the same key, which fits every lock, the system of locking is ruined by uniformity. And this is exactly what we have done in agriculture, with our use of a single vertical resistance in a uniform pure line, clone or hybrid cultivar that might be grown over a huge area as a homogeneous population. This was sub-optimization at its worst.

Auto-infection can be controlled only by horizontal resistance because auto-infection can commence only after there has been a matching allo-infection. Many crop parasites reproduce asexually to produce a clone. All the individuals within that clone have the same key which matches

the lock of the host and, consequently, all auto-infection is matching infection. Even parasites that reproduce sexually, such as many insects, will soon reach homozygosity of the matching biotype. However, vertical resistances against insects are rather rare, and this may explain why there has been so little crop breeding for resistance to insects pests.

These functions of the two kinds of resistance are emergent properties that were completely unknown until recently, and, being unknown, they were inevitably ignored by crop scientists during the twentieth century.

Another obvious example of sub-optimization occurs when breeding for a single resistance mechanism, such as hairy leaves that repel an insect pest. Horizontal resistance to insects usually consists of many obscure mechanisms, all of which may vary quantitatively, and which collectively reduce the rate of population growth of that pest.

The converse of sub-optimization is known as the holistic approach, which leads to local optimization of all variables. When breeding for horizontal resistance, therefore, we must not sub-optimize. We must work at the systems level of the agro-ecosystem. Within this agro-ecosystem, we must use population breeding to produce adequate and durable resistance to all locally important species of parasite, by exerting selection pressure for the one characteristic of 'good health'. Susceptibility to only one important species of parasite will result in an inferior cultivar, and this would constitute a clear case of sub-optimization. In addition to 'good health', new cultivars should have good levels of all the other variable attributes necessary to a productive agriculture. This approach does not necessitate participatory plant breeding, and some professional

breeders may choose to work on their own in a scientific institution. However, this approach does depend on high numbers of plants being screened, and many amateur breeders, working cooperatively with a professional, can lead to both greatly increased numbers of plants screened, and greatly increased attention applied to each plant screened.

15.4 BREEDING CROPS FOR DURABLE (HORIZONTAL) RESISTANCE

In this section there are inevitable generalizations that do not apply to all crop species. For example, comments about open-pollinated crops may not apply to self-pollinated crops, or comments about annual crops may not apply to perennial crops. When planning a breeding programme, therefore, readers should highlight only those aspects of these descriptions that apply to their crop species of choice.

15.4.1 Maize in tropical Africa

The best way to breed for horizontal resistance is to imitate the behaviour of open-pollinated maize (*Zea mays*) in tropical Africa, following the introduction of the re-encounter disease called Tropical rust (*Puccinia polysora*). A re-encounter parasite is one in which the host was separated from its parasite and taken to another part of the world. At a later date, the parasite is also taken to that new area where it re-encounters its host, which has lost resistance in the meanwhile. Conversely, a new encounter parasite is one which evolved separately from its host, on a botanical relative. Later the two are brought together in a new encounter. An old encounter parasite is one in which the host and parasite have never been separated, even though both may have been moved to new areas (Buddenhagen, 1987).

This crop is called corn in North America but it is called maize in all other countries, and in all other languages. It was taken by the Spanish from the New World to the Iberian peninsula some five centuries ago and tropical rust was either left behind or it failed to survive outside the tropics. The Portuguese then took rust-free maize to Africa and all points east, where it was cultivated for more than four centuries in the absence of tropical rust. This negative selection pressure led to the level of horizontal resistance to tropical rust declining to its minimum natural level. In technical terms, this is the Hardy-Weinberg equilibrium. In theory, it should be possible to breed experimentally for absolute susceptibility, but this is a somewhat academic point.

With the development of trans-Atlantic air transport in the 1940s, tropical rust was accidentally taken from the new world to the old. Devastating epidemics developed in the low altitude, equatorial tropics. In East Africa, a classic breeding programme for vertical resistance was initiated. Genes for resistance had to be imported from tropical America because none could be found in the local maize populations (Storey *et al.*, 1958). Unfortunately, these vertical resistances broke down so quickly that none lasted long enough to be released to farmers.

However, the appearance of this re-encounter disease exerted positive selection pressure for horizontal resistance in the farmers' open-pollinated crops. After about a dozen maize generations, the levels of disease had declined from 'total loss of crop' to 'negligible loss of crop'. The horizontal resistance had increased from its minimum level to its maximum level. With two crops each year, this transformation occurred in about six years, and it had happened without any help from plant

breeders or plant pathologists. It is common knowledge that this horizontal resistance has now endured for half a century without any suggestion of breaking down to new strains of the parasite.

15.4.2 The inactivation of vertical resistance

It is impossible to breed for horizontal resistance if the screening population is protected by functioning vertical resistances. In other words, it is possible to breed for horizontal resistance only *after* the vertical resistances have been matched.

There are several methods of ensuring that no vertical resistances are functioning during screening for horizontal resistance. The first method is to use only parents that possess no genes for vertical resistance. This is usually possible only in crops species that have had foreign vertical resistance genes inserted into them. For example, the vertical resistance genes to Late potato blight (*Phytophthora infestans*) were inserted into cultivated potatoes from the wild *Solanum demissum*.

In this context, it is important to note that vertical resistance genes occur only in seasonal tissues in which there is a discontinuous pathosystem. That is, in each new season, each host individual is free of the parasite and must be newly allo-infected. This situation is seen in the seasonal tissues of annual plants, or the leaves and fruits of deciduous trees and shrubs. Vertical resistances can also occur in the seasonal, aerial tissues of perennial crops such as hops and potatoes. But vertical resistances are not found in perennial crops such as sugar cane, cassava and sweet potato, or in evergreen tree crops such as olives, citrus, tea and cocoa. Apparent exceptions to this rule occur in Coffee leaf rust caused by *Hemileia vastatrix*, and South American

leaf blight of rubber, caused by *Microcyclus ulei*. However, coffee is functionally deciduous in the dry season with respect to rusted leaves only, and rubber is a deciduous species in spite of growing in the Amazon valley, which is permanently warm and wet.

The second method involves inactivation of any vertical resistance genes that may be present in the screening population. This is necessary in crops, such as wheat, in which it is extremely difficult, if not impossible, to find parents with no vertical resistance genes. This inactivation can be achieved with the 'one-pathotype technique'. The first step is to designate a single vertical pathotype of the parasite in question. Potential parents are then screened for susceptibility to this designated vertical pathotype. Only those lines that are susceptible to the designated vertical pathotype can become original parents of the screening population. All recombinations of the vertical resistance genes that occur in all subsequent breeding generations will then be matched by the designated vertical pathotype, which is used to inoculate each screening population. Amateur breeders will have difficulties with this somewhat complex but essential procedure, and in a participatory breeding programme it should be the responsibility of the breeder or pathologist. The details of the technique have been described elsewhere (Robinson, 1996, 2004).

A third possibility is to rely on natural matching of any vertical resistances that may be present in the screening population. Any individual that has no parasitism is inspected for the presence of the necrotic spots that are typical of a vertical resistance reaction, and affected individuals are discarded. However, this method can be very wasteful of breeding material if there are many such plants.

It is not clear whether the maize in tropical Africa lacked vertical resistance genes, or that it had such genes but their resistances were matched so quickly that they went unobserved. In either event, the positive selection pressure for horizontal resistance was not hindered by functioning vertical resistance.

15.4.3 Genetic resources

It is now a plant breeding shibboleth that breeding for resistance requires a 'good source' of resistance before the breeding can even begin. This is true when breeding for vertical resistance, because it is essential to have at least one gene for resistance. But it is *not* true when breeding for horizontal resistance. This point is so important that it merits careful explanation.

Consider a heterogeneous screening population in which every individual is different from every other individual, but in which all the plants are susceptible. Each plant possesses about 10 percent of the total polygenes that contribute to the horizontal resistances to each of the various locally important parasites. The host population as a whole is thus very susceptible. However, we may assume that each host individual possesses a different 10 percent of those total polygenes. Provided that there is a reasonably wide genetic base, this will mean that all the polygenes are present in the population, but their frequency is too low for much resistance to be expressed in any of the individuals. The objective of the breeding is to increase these resistance gene frequencies.

The most resistant plants are selected and they become the parents of the next screening generation. Now the most resistant individuals will possess perhaps 20 percent of the total polygenes. In the next screening generation, this percentage is even higher,

and with each breeding cycle the levels of horizontal resistance increase until no further increase is either possible or necessary. This process of quantitative increase, in which the progeny have a higher level of a quantitative variable than their parents, is known as transgressive segregation.

So, when breeding for horizontal resistance, there is no need to begin with a good source of resistance, but there must be a reasonably wide genetic base to ensure that all the necessary polygenes are present.

In practice, it is much easier to breed for horizontal resistance than it is to breed for high yield, high quality of crop product or high agronomic suitability. It is therefore best to use high-yielding, high-quality, agronomically suitable, but susceptible, modern cultivars as the original parents. With suitable selection procedures, it should be easy to gradually increase the levels of horizontal resistance, while retaining the other desirable qualities. Conversely, it would be very difficult to use highly resistant, primitive archetypes as the original parents, and then try to improve their various agricultural attributes, while retaining their resistance.

The maize of tropical Africa illustrated this point conclusively. The horizontal resistance accumulated within very susceptible host populations of highly prized local landraces. No 'good source' of resistance was necessary, and no diminution of the prized characteristics occurred. When breeding for horizontal resistance, therefore, the discernible qualities of the genetic resources must be those of yield, quality of crop product and agronomic suitability.

15.4.4 Population breeding

Recurrent mass selection means that a heterogeneous plant population is screened for the best individuals, which then become

the parents of the next generation. This process is repeated some 10–15 times, by which time the upper limits of most quantitative variables will have been reached. In each breeding cycle (i.e. each generation of recurrent mass selection), there should be at least 10 to 20 parents, depending on the nature of the crop. These parents may be randomly cross-pollinated, or hand-pollinated in all combinations, again depending on the nature of the crop.

Quantitative variables change as a result of selection pressures. The term 'pressure' is used in the sense of bringing pressure to bear, of coercion or persuasion, and selection pressures can be positive or negative.

Positive selection pressures lead to the increase of a variable, while negative selection pressures lead to its decrease. The mechanism of these changes is reproductive fitness. For example, if a heterogeneous host population is susceptible to a parasite, the most resistant individuals will be parasitized the least and will reproduce the most, while the most susceptible individuals will be parasitized the most and will reproduce the least. With each generation the population as a whole will gain resistance as a consequence of this positive selection pressure for resistance.

Conversely, if the parasite is absent from the locality in question, as with the maize of tropical Africa, or because of a functioning vertical resistance or the use of a pesticide (i.e. the vertifolia effect; see above), the selection pressure for horizontal resistance will be negative, and the frequency of genes controlling horizontal resistance will decrease. This happens because any unnecessary genetic characteristics tend to decline to a level called the Hardy-Weinberg equilibrium.

Positive selection pressure can be increased by increasing the ratio of selected

plants to total plants. This ratio is called the selection coefficient. In practice, this means that the screening population should be as large as possible so that perhaps only one plant in a thousand becomes a parent of the next generation. The possibilities depend very much on the nature of the crop. If the plants are small, such as wheat, rice or beans, it is entirely feasible to use a screening population of some 100 000 plants, but if the population is a tree crop, such as a fruit or nut species, such large populations are not feasible. However, the size of the screening population is not critical, and if a relatively small population is necessary because of land or labour restrictions, the breeding programme will require more time, but the deficiency will be no worse than this.

Should it transpire that the original genetic base was too narrow to accumulate adequate horizontal resistance, new genetic material can be added to the screening population. This may lead to an initial, slight loss of horizontal resistance, but the ultimate potential will be improved.

A special aspect of quantitative variables is that they must all be increased simultaneously. There is little point in having high levels of horizontal resistance to all of the locally important parasites except one. Even a single susceptibility will spoil a cultivar, and make spraying or some other form of artificial control necessary (see also sub-optimization, above). This is a major difference between breeding for single-gene and multiple-gene characters. Pedigree breeding allows the transfer of a single-gene character, such as a resistance, from a wild plant to a cultivar by hybridization and back-crossing. A multiple-gene variable cannot be transferred in this way because hybridization leads to an immediate dilution. Hence the need for

a simultaneous increase of all quantitative variables during population breeding.

Once the required levels of quantitative variables have been reached, steps can be taken to produce pure lines, clones, or synthetic or hybrid varieties, according to the requirements of the crop in question.

The maize of tropical Africa provided good examples of both negative and positive selection pressures to tropical rust. It also illustrated the need for horizontal resistance to all locally important parasites, because subsistence farmers do not use pesticides on their food crops.

15.4.5 Male gametocides

A male gametocide is a chemical that makes a plant male-sterile but female-fertile. By using male gametocides in a screening population, inbreeding plants, such as wheat, can be converted to outbreeders. A wheat population then becomes the equivalent of a maize population, with unsprayed plants acting as male parents. This can be very useful as it eliminates the laborious and severely limiting process of cross-pollinating by hand. Working this way in Brazil, Beek (1988) obtained millions of wheat crosses with only an hour or two of work.

The details of male gametocides are beyond the scope of this chapter and amateur breeders who decide to use these chemicals should get the advice of the specialists who are cooperating in the participatory plant breeding.

15.4.6 Screening existing populations

With some crops, particularly tree species, it is possible to find all the resistance we need by screening existing, heterogeneous populations. This was possible with coffee in Ethiopia (see below). There is then no need for a formal breeding programme as such. Other tree crops in which such an

approach is feasible include cocoa (Witch's broom disease caused by *Crinipellis pernisciosa*) and rubber (South American leaf blight caused by *Microcyclus ulei*) in the Amazon valley, tea (Blister blight caused by *Exobasidium vexans*) in India, date palms (Bayoud disease caused by *Fusarium oxysporum* f.sp. *albedinis*) in North Africa, coconut (Cadang-Cadang disease) in the Philippines, white pines (Blister rust caused by *Cronartium ribicola*) in North America, and many other plantation forest species.

15.4.7 Negative screening

Negative screening means that you identify the worst individuals in a population and remove them, rather than identifying the best individuals and keeping them. Negative screening can be useful in two situations. The first occurs when there is a danger of cross-pollination from undesirable individuals in a screening population, such as open-pollinated crops, or self-pollinated crops in which the mother plants have been treated with a male gametocide. These undesirable male individuals must be identified and either removed or deflowered.

A similar situation occurs when a heterogeneous population of an open-pollinated annual crop, such as alfalfa, is being improved during the process of seed production. It is often more profitable to remove the relatively few individuals that show the most susceptibility, than it is to collect the individuals that show the most resistance. This negative selection should obviously be conducted before cross-pollination becomes possible.

Negative screening can also be used profitably in a heterogeneous tree crop. For example, a crop of cocoa might be heavily diseased with Witch's broom disease (*Crinipellis pernisciosa*). A small percentage of the trees are highly susceptible and

are infecting all the other trees. If the most susceptible trees are identified and removed, and all other diseased branches are also removed, this parasite interference (see above) will stop and the disease will be controlled. Even if the disease is merely reduced in intensity, further negative screenings of the most susceptible trees will eventually control the disease. This procedure is often far more economical than a positive screening for resistant trees, followed by a subsequent replanting of the entire crop with these selections.

15.4.8 On-site selection

The maize of Africa illustrated the importance of on-site selection (see above). *Puccinia polysora* has maximum epidemiological competence at the equator, and at sea level. As latitude increases, the epidemiological competence decreases to nothing at sea level at the tropics of Cancer and Capricorn. As altitude increases, the epidemiological competence decreases to nothing at the equator at elevations of about 1 200 m.

Maize from the highlands of Kenya, where tropical rust lacks epidemiological competence entirely, is extremely susceptible when planted at sea level near the equator. Conversely, maize in Malawi was reported to be highly resistant to tropical rust but it proved to be very susceptible when planted near the equator at sea level. This was environmental erosion that occurred because the maize had come from an area of minimum epidemiological competence of the pathogen, where it had suffered minimum selection pressure for resistance. When planted in an area of maximum epidemiological competence, its susceptibility was revealed.

Because this maize in tropical Africa was cultivated as an open-pollinated crop, each

farmer's crop constituted a natural screening population. Each farmer's maize then constituted a landrace with exactly the right amount of horizontal resistance to tropical rust for that latitude and that altitude. This was an example of subconscious selection

Because tropical rust is so sensitive to altitude and latitude, the pathosystems, and hence the agro-ecosystems, of tropical rust are small. However, this extreme of environmental sensitivity is unusual, and with most crop species the agro-ecosystems are quite large, and relatively few breeding programmes are necessary.

15.4.9 A holistic approach

The tropical maize in Africa also illustrates the need for a holistic approach. Before the appearance of tropical rust, the maize had no important pests or diseases. In other words, it had high levels of comprehensive horizontal resistance. That is, it had adequate levels of horizontal resistance to all the locally important parasites. With the introduction of this re-encounter parasite, this pathosystem balance was immediately lost, and it required about a dozen generations of selection to restore it.

It can be argued that pathosystem balance has been lost in virtually all of our modern crops. The objective of participatory plant breeding should be to restore pathosystem balance in each crop species in each agro-ecosystem. When we consider the many different crops and the many different agro-ecosystems worldwide, this is too big a task for professional plant breeders to undertake on their own, and it is perhaps the best justification of participatory plant breeding.

15.4.10 Selection pressures for other qualities

If we were to produce new cultivars that had high levels of horizontal resistance to all

locally important parasites, but which had reduced yield and quality of crop product, we would be sub-optimizing (see above). This is why we should use modern but susceptible cultivars as our genetic resource. It is clear that a good source of resistance is not necessary when breeding for horizontal resistance, but that high yield, quality and agronomic suitability are necessary. The levels of various horizontal resistances are increased while selection pressures for yield and quality are maintained to ensure that these qualities are not reduced.

15.4.11 Measurement of horizontal resistance

When measuring the results of breeding for horizontal resistance, assessments can be relative only. That is, we can say that a new cultivar has either greater or less horizontal resistance to a particular parasite than another well known and well tried cultivar. An alternative description can be given with the phrase ‘spraying not necessary’, but even this must be qualified with the rider that this is only true in a normal season.

15.4.12 Crops that are difficult or impossible to breed

For technical reasons, some crops are difficult or even impossible to breed, and amateur breeders should not attempt to improve them. These include banana, citrus, date palm, figs, garlic, hops, horseradish, olives, pineapple, sisal and wine grapes. However, most of the main food crops are easy to breed, and none of them could be described as being difficult to breed. Worldwide, it is clearly logical for amateur plant breeders to work with participatory plant breeding of crops that are easy to breed, while the professional plant breeders should work with crops that are difficult to breed.

15.5 EXAMPLES OF BREEDING FOR HORIZONTAL RESISTANCE

Simmonds (1991) has compiled a comprehensive review of the results of breeding for horizontal resistance. He gives examples of durable resistance in 21 species of crop, functioning variously against airborne and soil-borne pathogens—fungal, bacterial, viral, insect and nematode. Stoner (1992) reviewed 705 papers on host resistance to insects and mites in vegetables, and she also quotes reviews of this topic in grain crops, alfalfa and cotton. She comments that, in most studies, the resistance is a quantitative trait, but she adds that there has been little plant breeding for resistance to insects.

15.5.1 Potatoes in Kenya, Mexico, Scotland and the United States of America

John S. Niederhauser was one of the pioneers of horizontal resistance. Indeed, he was the first scientist to reject the use of vertical resistance in favour of horizontal resistance, and he did this in Mexico with resistance to Late blight of potato (*Phytophthora infestans*). His most famous cultivar was Atzimba, and Mexican scientists have continued his work. Blight is so severe in Mexico that the popular cultivar Alpha has to be sprayed with fungicides 25 times each season. The new, horizontally-resistant cultivars, such as Sangema and Tollocan, need to be sprayed only once or twice each season.

Working in Scotland, Simmonds (1976) demonstrated that the potatoes cultivated in Europe (*Solanum tuberosum*) were derived from the *S. andigena* of South America. With only four generations of recurrent mass selection he was able produce ‘*neo-tuberosum*’ from *S. andigena*, and he was also able to accumulate useful levels of horizontal resistance to Late blight.

In Kenya, Robinson (1996) attempted to imitate the maize of tropical Africa when breeding potatoes for horizontal resistance to both Late blight (*Phytophthora infestans*) and Bacterial wilt (*Pseudomonas solanacearum*). He was able to have two breeding cycles each year with 150 000 seedlings in each cycle. When his cultivar Kenya Baraka was released to farmers, the annual potato production of this country increased from less than 10 000 t in 1974, to an estimated 1 million tonnes in 2004. This production was possible without any use of crop protection chemicals, and without any renewal of seed stocks by the use of certified seed tubers. It should be noted, however, that the temperate viruses of potato lack epidemiological competence in this country, and the Colorado beetle (*Leptinotarsa decemlineata*) is absent.

In the United States of America, Fisher, Deahl and Rainforth (2002) have been breeding potatoes for horizontal resistance to Colorado beetle (*Leptinotarsa decemlineata*) of potatoes and have made useful progress after only a few generations of recurrent mass selection. No single-gene resistances occur against this insect parasite, and this is apparently the first serious attempt to breed for resistance to it in more than a century.

15.5.2 Coffee in Ethiopia

Arabica coffee (*Coffea arabica*) is apparently an allo-tetraploid that was derived from two diploid species in the area of modern Uganda in about 650 CE. It soon died out in its centre of origin, but it was taken at an early date to Ethiopia, which became the centre of diversification. A pathogen (*Colletotrichum coffeanum*) of modern coffee, which causes Coffee berry disease, was left behind, and Ethiopia remained free of this disease until 1970, when this re-

encounter parasite was inadvertently introduced. The coffee crops of Ethiopia were heterogeneous, and trees with the minimum horizontal resistance lost all their berries three months before harvest. Trees with the maximum horizontal resistance lost no berries at the time of harvest, and they occurred with a frequency of about one in a thousand. The overall effect was an average yield loss of 40 percent, and this destroyed the economic viability of this crop.

About half-a-million trees were examined and 650 resistant individuals were identified. Their first harvests were kept for seed, and about 1 000 seedlings were germinated from each tree. The first screening criterion was for homozygosity, and only those trees that were 'breeding true' were kept. (*Coffea arabica* is self-pollinating, with about 3 percent of out-crossing). Other tests included yield, cup quality and resistance to other pests and diseases. The best 25 lines became available as new cultivars for farmers only eight years after the programme was initiated (Robinson, 1996).

15.5.3 Beans in Mexico

Roberto Garcia Espinosa has been using recurrent mass selection on black or common beans (*Phaseolus vulgaris*) in Mexico with a view to increasing the levels of horizontal resistance to all locally important parasites. Commercial crops will yield up to 1 500 kg/ha if they are properly protected with fungicides and insecticides. Beans from the seventh breeding cycle of the recurrent mass selection programme yield 2 400 kg/ha without any use of crop protection chemicals. This work has yet to be scientifically described (Roberto Garcia Espinosa, pers. comm., 2007).

15.5.4 Sugar cane in Hawaii

For many years, the sugar cane breeders of Hawaii differed from all other cane

breeders in that they used recurrent mass selection. They produced about three million seedlings in each breeding cycle. These would be reduced to about 600 000 on the basis of visual appearances only. The survivors would be tested for sucrose content, with further massive reductions in numbers. As the number of survivors decreased, the complexity of the tests could be increased. The final result is that Hawaiian sugar cane yields twice as much as any other country, and it does this without any use of crop protection chemicals, other than to protect the cut surfaces of the cane setts used for planting.

15.5.5 Sweet potatoes in United States of America

Jones, Dukes and Cuthbert (1976) were among the pioneers of horizontal resistance breeding when they worked with sweet potato (*Ipomoea batatas*) in South Carolina. They used recurrent mass selection and accumulated good levels of horizontal resistance to several species of insect pests and fungal parasites, as well as improvements in yield and quality. This is an easy crop to work with as it possesses no vertical resistance genes.

15.5.6 Wheat in Brazil

Beek (1988) attempted recurrent mass selection with wheat in Brazil, using male gametocides to achieve large numbers of random cross-pollinations. He used hydroponics and single-seed descent to allow late selection. He made good progress in accumulating horizontal resistance to a number of wheat parasites but he was unable to complete his programme. Specialists advising amateur breeders in a participatory wheat breeding project should regard Beek's report as essential reading.

15.6 ANCIENT CLONES

Ancient clones obviously have high levels of horizontal resistance to all their parasites, and this resistance has endured for centuries, even millennia, in crops such as aroids, bananas, dates, figs, garlic, ginger, hops, horseradish, olives, peppercorns, pineapple, saffron, sisal, turmeric, vanilla, wine grapes and yams. Some of these clones, such as wine grapes, dates and bananas, are now severely parasitized in some areas, but this is only because of new-encounter, foreign parasites.

15.7 AUTOCRATIC AND DEMOCRATIC PLANT BREEDING

Breeding for vertical resistance is highly technical, expensive, difficult, and repetitious. It usually requires a team of scientists working in a large institute. Inevitably, given these problems, fewer cultivars are produced than with population breeding, and it is important that these cultivars have a wide agro-ecological adaptability so that they can be used over as wide an area as possible. Vertical resistance usually has a very wide adaptability and, coupled with its complete control of a parasite, this makes it an attractive plant breeding approach.

Vertical resistance breeding was typical of the green revolution, and the high yielding, 'miracle' wheats and rices. While there is no question that the increased yields of these cultivars have saved about a billion human lives, the fact remains that farmers had little choice of cultivar because there were relatively few of these high-yielding cultivars available. A further disadvantage was that those cultivars that were available were liable to fail when their vertical resistances broke down. Breeding for vertical resistance also makes farmers totally dependent on the formal seed system.

This approach might be termed 'autocratic' plant breeding, because it is the

breeder, rather than the farmer, who decides what kind of cultivar is to be bred, and which cultivar is to be grown. Its converse is ‘democratic’ plant breeding, in which the farmer participates in the breeding, has a choice of resistance type, has a wide choice of cultivars, and can make their own decisions concerning which cultivars to grow. Democratic plant breeding is possible with horizontal resistance, which is so easy to use that it can be employed by numerous amateur breeders, who cooperate with professionals in participatory plant breeding and plant breeding clubs.

15.7.1 Plant breeding clubs

Plant breeding clubs are made up of amateur breeders, who might be hobby gardeners, environmentalists, green activists, farmers, students or even schoolchildren. Each club is independent and free to breed any crop it chooses, for any improvements it chooses and using any breeding methods it chooses. Their primary objective is likely to be the production of new cultivars with sufficient horizontal resistance to permit cultivation without any crop protection chemicals, and without any reduction in yield, quality or agronomic suitability. This is because breeding for durable, horizontal resistance is so easy when compared with breeding for the ephemeral, but complete, vertical resistance.

Plant breeding clubs are particularly useful with participatory plant breeding. A group of sympathetic crop specialists can cooperate with several plant breeding clubs, consisting of various categories of amateur breeders. Possibly the most effective clubs are university plant breeding clubs made up of student-breeders assisted by professors. Greater details have been provided by Robinson (2004).

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Breeding for quantitative variables

Part 3: Breeding for resistance to abiotic stresses

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16.1 INTRODUCTION

Plant breeding has been very successful in environments that are either naturally favourable or that can be made profitably favourable by irrigation and fertilizer and by chemical control of pests and diseases.

Cox *et al.* (1988) estimated that the annual genetic gains in bread wheat in the United States of America from 1917 to 1987 have been 16 kg/ha/yr. Russell (1984) found that the genetic gain in maize hybrids released between 1930 and 1980 was 54.2 percent. Austin, Ford and Morgan (1989) estimated 38 kg/ha/yr for the genetic gain between 1908 and 1985 in wheat in the United Kingdom. Similar examples are available in many other crops.

By contrast, yield improvements have been very elusive in marginal environments, to the extent that the role of breeding for those environments is often questioned. What it is not questioned is why it has not been possible to improve agricultural production by simply transferring into marginal environments cultivars or methodologies that have made breeding for favourable conditions so successful. As a result, the yield of some important staple crops has shown only modest increases or remained virtually unchanged (Ceccarelli and Grando, 1996; Ceccarelli *et al.*, 2004). This has been attributed to the difficult nature of the target environments where yields have shown little increase (Passioura, 1986; Blum, 1988) and has been accepted as inevitable. Therefore, most of the selection work in breeding programmes is done in favourable conditions (Simmonds, 1991), and much research has been done, and resources expended, to seek alternatives to empirical breeding for unfavourable conditions, such as analytical breeding and, more recently, molecular breeding. Much less has been done on assessing whether a

paradigm shift was needed when selecting for abiotic stresses.

One hypothesis is that cultivars often defined as 'widely adapted' are actually specifically adapted to conditions that are at or near the optimum for crop growth. Therefore the superiority they have in these environments is lost in suboptimal environments.

The objective of this chapter is to discuss critical problems associated with breeding for abiotic stresses, to analyse possible reasons for the limited success breeding has had in stressed environments, and to indicate that participatory plant breeding is one way to overcome the inherent difficulties. Most examples are derived from ICARDA's barley breeding programme for low-rainfall areas.

16.2 MOST COMMON ABIOTIC STRESSES

Abiotic stresses are consequences of extremes of physical environment comprising climatic stresses, such as drought, flood, heat and cold; and soil or water conditions, such as salinity, metal toxicity and nutrient deficiency. Plants can experience abiotic stresses resulting from the shortage of an essential resource, or from a toxic excess of a substance, or from climatic extremes. In some cases the same resource can impose stress both when in shortage and when in excess (i.e. water and temperature). Occurrence, severity, timing and duration of stresses vary from location to location, and in the same location from year to year. In the case of drought, cultivars successful in one dry year may fail in another, or cultivars resistant to terminal drought may not be resistant to intermittent drought, or to drought occurring early in the season (Turner, 2002). In addition, abiotic stresses seldom occur in

isolation; they often interact, both with other abiotic stresses and with biotic stress. Moreover, areas with a high probability of abiotic stresses generally have low-input agriculture (Cooper *et al.*, 1987), because the risk of losing the crop or of a low yield discourages the farmers from using costly inputs, particularly fertilizers. This results in low outputs, poor human nutrition and reduced educational and employment opportunities, especially for girls. The rural poor are particularly badly affected because of lack of access to alternative sources of employment or food.

16.2.1 Drought

Drought, defined as water availability below that required for maximum crop yield, is one of the main factors limiting crop production. Although it reaches the front pages of the media as drought warnings or when it causes famine and death, drought is a permanent constraint to agricultural production in many developing countries, and an occasional cause of losses in agricultural production in developed ones. Several drought warnings have been issued in recent years in Australia, Europe and the United States of America. Climate changes will increase the frequency of droughts, particularly in Southeast Asia and Central America, and by 2050 are expected to cause water shortages for 67 percent of the future population in the world (Ceccarelli *et al.*, 2004).

In areas where water availability is limited, and irrigation is not available, the choice of crops is restricted to a few, and often to only one, thus making farmers in those areas vulnerable for lack of options. In fact, most of the rural poor live in areas where crop productivity and crop diversification are limited by lack of water. Therefore it is not surprising that there is an ongoing global research effort on social,

agronomic, genetic, breeding, physiological and molecular aspects of drought resistance, or as recently more often used, water productivity (Passioura, 2006). This is highlighted by the publication of several reviews (Ceccarelli *et al.*, 2004; Reynolds, Mujeeb-Kazi and Sawkins, 2005; Parry, Flexas and Medrano, 2005).

Drought has been always a challenge to plant breeders, despite many decades of research (Blum, 1993). The development, through breeding, of cultivars with higher and stable harvestable yield under drought conditions would be a major breakthrough (Ceccarelli and Grando, 1996). However, drought resistance is a very elusive trait from a genetic point of view. This is because the occurrence, severity, timing and duration of drought vary from year to year, and although every year there are “winners”, it is difficult to find those that are consistently successful. To make matters worse, drought seldom occurs in isolation; it often interacts with other abiotic stresses (particularly temperature extremes), and with biotic stress. As mentioned earlier in this chapter, the risk of losing the crop because of drought limits the use of inputs.

Also the definition of dry areas seems to be an elusive issue. This is illustrated by the distribution of crops in different agro-climatic environments. For example, in a country such as the Syrian Arab Republic, with a large spatial variability of rainfall within short distances (van Oosterom, Ceccarelli and Peacock, 1993), bread wheat (*Triticum aestivum* L.), durum wheat (*T. turgidum* var. *durum* L.) and barley among the cereals, and faba bean (*Vicia faba* L.), chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* L.) among the food legumes, are grown in progressively drier environments, with some overlapping. Therefore, a dry area for faba bean or bread

wheat is moderately favourable for durum wheat and chickpea, and a dry area for durum wheat and chickpea is moderately favourable for barley and lentil.

At the drier end of the spectrum, barley and lentil are the only rainfed crops, and the other cereals or legumes are only grown under supplementary or full irrigation. The situation described for the Syrian Arab Republic applies to most countries of the Mediterranean basin and West Asia, and for crops such as millet, sorghum and maize to the dry areas of the tropics, and is only altered by irrigation.

The complexity of breeding for dry areas is not only due to the biological complexity of drought resistance, but also to the consequences of drought for the livelihood of people living in the dry areas. In developed countries, farmers have various forms of social protection against the devastating effects of drought, while in developing countries farmers have to survive on their own, usually selling their assets, most commonly livestock. In areas affected by drought in developed countries farmers may prefer cultivars capable of high yields in the few favourable years; this is very different in the dry areas of most developing countries with no or little social assistance where farmers prefer varieties capable of some yields even in the driest years. This is an example that the same biological problem in different social contexts requires different solutions.

16.2.2 Soil toxicities and deficiencies

Soil plays a major role in determining the amount and availability of nutrients and toxic minerals. Soil toxicities and deficiencies render more than one hundred million hectares of agricultural land marginal for agriculture, limiting production and creating poverty for millions.

Soil mineral stresses are increasingly becoming important limiting factors for crop plants in many parts of the world. Acid soil and associated aluminum toxicity affect over 2 billion hectares worldwide (Humphreys and Humphreys, 2005). Mineral nutrient deficiency can be caused by low nutrient status of the soil, low mobility or availability of nutrients within the soil.

Salinity is generally defined as the presence of excessive amount of soluble salts that hinder or affect the normal function of plant growth (Shafiq-ur-Rehman, Harris and Ashraf, 2005). Saline soils have a mixture of chloride salts, with sodium chloride being often dominant. Salinity can be divided into primary sources in soils derived from saline parent rocks (Sposito, 1989) and secondary salinization caused by human intervention, such as irrigation (Sposito, 1989).

Salinization is one of the most common forms of soil degradation. Almost all continents have problems related to saline soils (Pessarakli, 1999), and is particularly severe in arid and semi-arid regions.

It is estimated that 6 percent of the world's land and 30 percent of the world's irrigated areas already suffer from salinity problems (Unesco Water Portal, 2007).

16.2.3 Temperature stresses

Temperature extremes can be experienced on both a daily or seasonal basis. Long-term climatic changes lead to higher average temperatures and increase the frequency and severity of extreme temperature events. As with other stresses, early and late stages of crop growth are particularly sensitive to temperature extremes. Plants can be affected by exposure to prolonged periods of moderately high temperatures as well to short periods of extremely high tempera-

tures. Low temperatures can affect plants by chilling, which leads to physiological and developmental abnormalities, and by freezing, which causes cell damage. About 15 percent of arable land is estimated to be affected by freezing stress (Dudal, 1976).

Changes in temperature are the most certain aspect of climate changes. The most recent evidence from the Fourth Assessment Report on Climate Change of the Intergovernmental Panel on Climate Change (IPCC), published in 2007, indicates that the warming of the climate system is unequivocal, as it is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level. This is shown by (i) 11 of the last 12 years (1995–2006) rank among the twelve warmest years in the instrumental record of global surface temperature (since 1850); (ii) the temperature increase is widespread over the globe, and is greater at higher northern latitudes; (iii) global average sea level has risen since 1961 at an average rate of 1.8 mm/yr, and since 1993 at 3.1 mm/yr, with contributions from thermal expansion, and melting glaciers, ice caps and the polar ice sheets; and (iv) observed decreases in snow and ice extent are also consistent with warming. Satellite data since 1978 show that annual average Arctic sea ice extent has shrunk by 2.7 percent per decade, with larger decreases in summer of 7.4 percent per decade. Mountain glaciers and snow cover on average have declined in both hemispheres.

The 2007 report indicates that it is also very likely that over the past 50 years, cold days, cold nights and frosts have become less frequent over most land areas, and hot days and hot nights have become more frequent, and it is likely that heat waves

have become more frequent over most land areas, the frequency of heavy precipitation events has increased over most areas, and since 1975 the incidence of extreme high sea level has increased worldwide.

In conclusion, higher temperatures are part of the future climate for which breeders should breed today.

16.3 CHALLENGING CONVENTIONAL BREEDING CONCEPTS

Most plant breeders assume that it is too slow and too difficult to breed for environments where droughts or other stresses are unpredictable and variable. The target is hard to define, and heritability, and hence response to selection, is too low to achieve meaningful results. Therefore most of the breeding for stress environments has been actually conducted using the same basic approach that has been very successful in areas where lack of water or other abiotic stresses is seldom important.

With few exceptions, most breeding programmes share the following concepts:

- selection has to be conducted under the well-managed conditions of research stations. It is felt that environmental noises can be kept under control, error variances are smaller and response to selection higher;
- cultivars must be genetically homogenous (pure lines, hybrids, clones) and must be widely-adapted over large geographical areas;
- locally-adapted landraces must be replaced because they are low yielding and disease susceptible;
- seed of improved cultivars must be disseminated through mechanisms and institutions such as variety release committees, seed certification schemes and governmental seed production organizations; and

- the end users of new varieties are not involved in selection and testing; they are only involved at the end of the consolidated routine (breeding, researcher-managed trials, verification trials), to verify if the choices made for them by others are appropriate or not.

Breeders have very seldom questioned these assumptions. When they have, it has been found that:

- selection in well-managed research stations tends to produce cultivars that are superior to local landraces only under improved management—not under the low-input conditions typical of the farming systems of stress environments. The result is that although many new varieties outyield local landraces on a research station and some are released, few if any are actually grown by farmers in difficult environments;
- poor farmers in stress environments tend to maintain genetic diversity in the form of different crops, different cultivars within the same crop or heterogeneous cultivars, or combinations, to maximize adaptation over time (stability), rather than adaptation over space (Martin and Adams, 1987a). Diversity and heterogeneity serve to disperse or buffer the risk of total crop failure due to environmental variation. This is in sharp contrast to the trend of modern breeding towards uniformity;
- resource-poor farmers seldom use the formal seed-supply systems. They frequently rely on their own or on neighbours' seed (Almekinders, Louwaars and de Bruijn, 1994). Therefore, when the appropriate cultivar is selected, adoption is much faster through non-market methods of seed distribution (Grisley, 1993); and
- when farmers are involved in the selection process, their selection criteria

may be very different from those of the breeder (Hardon and de Boef, 1993; Sperling, Loevinsohn and Ntabomvura, 1993). Typical examples are crops used as animal feed, such as barley, where breeders often use grain yield as the sole selection criterion, while farmers are usually equally concerned with forage yield and the palatability of both grain and straw.

Although the chapter is largely based on the strategies and methodologies developed during the last 20 years in the ICARDA barley breeding programme, we believe that the main findings have general applicability. They will be described to demonstrate that it is indeed possible to improve the production of a typically low-input crop such as barley, grown in environments with low and poorly-distributed rainfall, low temperatures in winter, high temperatures and drought during grain filling, low soil fertility and poor agronomic management. The data were mainly obtained from three locations in the northern Syrian Arab Republic (Tel Hadya, Breda and Bouider). They represent three distinct agricultural systems. Tel Hadya (348 mm average annual rainfall) is a favourable high-input environment that lends itself to a wide choice of different crops. Bouider (236 mm average annual rainfall) represents the opposite extreme: a typical low-input, high-risk environment where barley is the only possible rainfed crop. Breda (273 mm average annual rainfall) is intermediate between the two, located on the edge of the area where Arabi Aswad becomes the dominant landrace. The three sites are geographically close, located 35 (Tel Hadya), 60 (Breda) and 80 km (Bouider) south-east of Aleppo. The key aspects of these strategies and methodologies are: (i) direct selection for specific adaptation in the target

environment (Chapter 9 in this volume); (ii) use of locally-adapted germplasm; (iii) use of plot techniques and experimental design to control environmental variation (Chapter 3); (iv) participation of farmers in selection; and (v) reliance on the informal seed-supply system to make the seed of new cultivars available to farmers (Chapter 21).

16.4 TYPE OF GERmplasm

In breeding for resistance to abiotic stresses there are certain types of germplasm—landraces, wild relatives or wild progenitors—that, although of limited or no value in breeding for favourable, potentially high-yielding conditions, may play a fundamental role in the success of a breeding programme. In many developing countries, landraces (also called farmers' varieties, old cultivars or primitive cultivars) are still the backbone of agricultural systems in unfavourable environments (Ceccarelli, 1984; Grando, von Bothmer and Ceccarelli, 2001). In these environments, the replacement of these cultivars has proved to be a difficult task. The reasons why farmers still prefer to grow only landraces or continue to grow landraces even after partial adoption of modern cultivars are not well documented, but include quality attributes such as food and feed quality, and seed storability (Brush, 1999). Landraces are often able to produce some yield even in difficult conditions, whereas modern varieties are less reliable. For example, where farmers have adopted modern cultivars they also have retained the landraces on the most unfavourable areas of the farm (Cleveland, Soleri and Smith, 2000).

Landraces of self-pollinated species are mixtures of a great number of homozygote genotypes (Brown, 1978, 1979; Ceccarelli and Grando, 1999; Grando, von Bothmer and Ceccarelli, 2001). Such evidence is

available in many crops, such as lentil (Erskine and Choudhary, 1986), sorghum (Blum, Golan and Mayer, 1991), bread and durum wheat (Porceddu and Scarascia Mugnozza, 1984; Damania and Porceddu, 1983; Spagnoletti-Zeuli, De Pace and Porceddu, 1984; Damania, Jackson and Porceddu, 1985; Lagudah, Flood and Halloran, 1987; Blum *et al.*, 1989; Elings and Nachit, 1991), beans (Martin and Adams, 1987a, 1987b), barley (Ceccarelli, Grando and van Leur, 1987; Weltzien, 1988; Asfaw, 1989; Weltzien and Fishbeck, 1990) and others. Therefore landraces contain a large amount of readily-usable genetic variation. Selection within landraces is one of the easiest, oldest and cheapest methods of plant breeding. In most cases, any interest shown by researchers in the variability of landraces has been academic; we know of few cases in which the variability has actually been used in breeding programmes. Yet, as mentioned before, the use of the variability of landraces in the area where landraces are adapted is a cheap and easy way to make progress.

At ICARDA we have used a large collection of barley landraces made in 1981 in the Syrian Arab Republic and Jordan (Weltzien, 1982). The collection was made by visiting the fields of 70 farmers and collecting 100 individual heads in each field. Cvs. Arta, Tadmor and Zanbaka are three examples of pure lines identified so far from two widely grown Syrian barley landraces (Tables 16.1 and 16.2).

In developed countries, landraces have been the basic material for genetic improvement in many crops until about 50 years ago. In these countries, however, the identification of superior genotypes has probably led many breeders to concentrate their attention on those few genotypes and this has resulted in: (i) the use of relatively

TABLE 16.1

Grain yield (t/ha) of Tadmor and Zanbaka in 11 and 8 locations respectively in the northern Syrian Arab Republic

Year	Location (Province)	Arabi Aswad	Tadmor	Zanbaka
1991	Shurkrak (Raqqqa)	0.220	0.130	-
	Al Ayouj (Raqqqa)	0.260	0.270	-
	Beer Asi (Raqqqa)	0.180	0.170	-
1992	Bylounan (Raqqqa)	0.640	0.940	1.100
	Masadeih (Hassake)	1.350	1.600	1.330
1993	Bylounan (Raqqqa)	0.792	1.176	1.132
	Shurkrak (Raqqqa)	0.666	1.268	0.916
1994	Bylounan (Raqqqa)	0.360	0.575	0.530
	Al Wastah (Raqqqa)	0.560	0.570	0.650
	Tell Hamzeh (Hassake)	0.812	0.876	1.250
	Al Hamar (Hassake)	1.100	1.000	0.650
Mean		0.631 (0.780)	0.780	0.945
% increase over Arabi Aswad		23.6	22.4	

Notes: The mean in parentheses is calculated from the locations in common with Zanbaka. The data are from trials conducted in farmers' fields, without fertilizer.

TABLE 16.2

Grain yield (t/ha) of Arta in 51 locations over seven cropping seasons

Year	No. of sites	cv. Arta	cv. Arabi Abiad	% increase
1986–1987	1	3.738	2.929	27.6
1988–1989	5	1.814	1.530	18.6
1989–1990	8	2.044	1.747	17.0
1990–1991	11	2.388	2.187	9.2
1991–1992	17	3.336	2.455	35.9
1992–1993	5	2.551	1.958	30.3
1993–1994	4	1.160	1.069	9.4

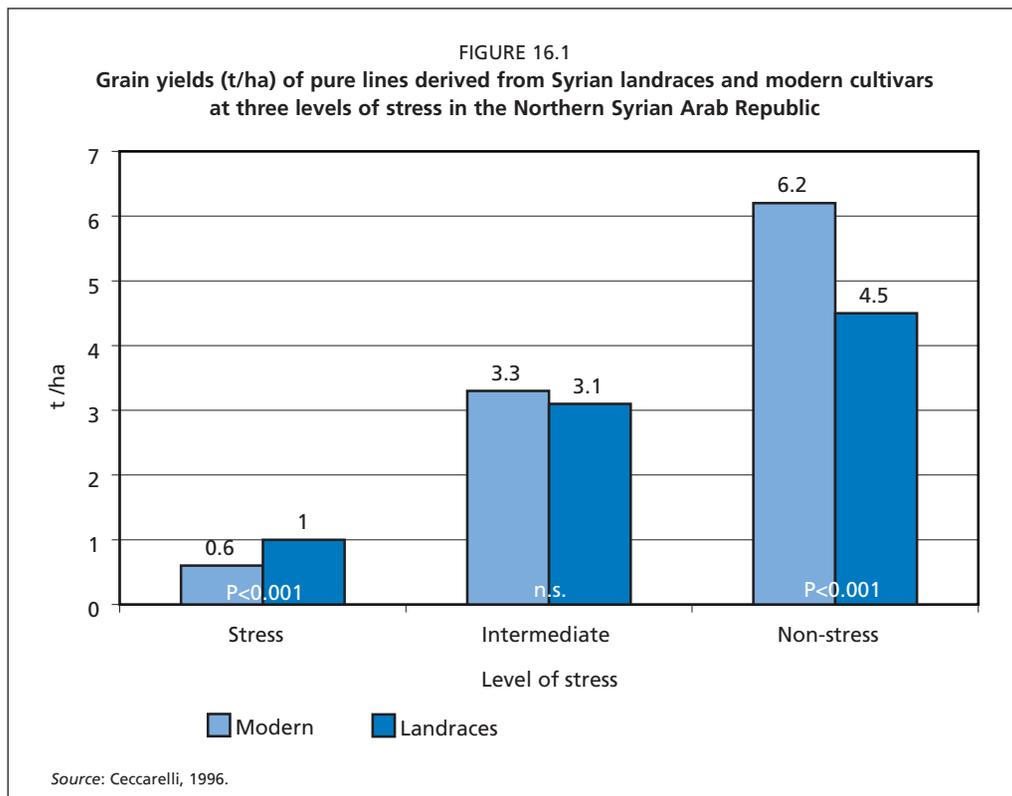
Note: The data are from trials on farmers' fields in the Syrian Arab Republic (except those of 1986–1987, which are from Breda research station).

few parents, leading to a considerable reduction of genetic diversity; and (ii) the loss of most of the landraces before they could be collected and conserved in germplasm banks, and (probably) before assessing whether their potential had been fully exploited.

The value of landraces as sources of drought tolerance is well documented in the case of barley in the Syrian Arab Republic (Grando, von Bothmer and Ceccarelli, 2001; Comadran *et al.*, 2008; Pswarayi *et al.*, 2008) and in several other crops elsewhere (Brush, 1999).

The comparison between barley landraces and modern cultivars under a range of conditions, from severe stress (low input and low rainfall) to moderately favourable conditions (high inputs and high rainfall), has consistently indicated that:

- landraces yield more than modern cultivars under low-input and stress conditions (Figure 16.1);
- the superiority of landraces is not associated only with mechanisms to escape drought stress, as shown by their heading date;



- within landraces there is considerable variation for grain yield under low-input and stress conditions, but all the landrace-derived lines yield something, while most modern cultivars fail;
- landraces are responsive to both inputs and rainfall and the yield potential of some lines is high, though not as high as modern cultivars; and
- it is possible to find modern cultivars that under low-input and stress conditions yield almost as well as landraces, but their frequency is very low.

The data in Figure 16.1 also suggest that selection conducted only in high-input conditions is likely to miss most of the lines that would have performed well under low-input conditions. Figure 16.1 also shows that the assumption of most breeding programmes that landraces are genetically infe-

rior is based on work conducted in research stations. Even those breeding programmes addressing target environments that have low yield potential because of the combination of biotic and abiotic stresses have rarely challenged this assumption.

The superior performance of landraces in dry areas is also evident from the frequency with which they are selected by farmers (Figure 16.2). The data in Figure 16.2 also show the importance and the role that the wild relatives, in this case the wild progenitor of cultivated barley, *Hordeum spontaneum*, have as a source of resistance to extreme levels of drought (Grando, von Bothmer and Ceccarelli, 2001; Ceccarelli *et al.*, 2004).

Gas exchange observations made at anthesis in a wet site showed that *H. spontaneum* had widely open stomata,

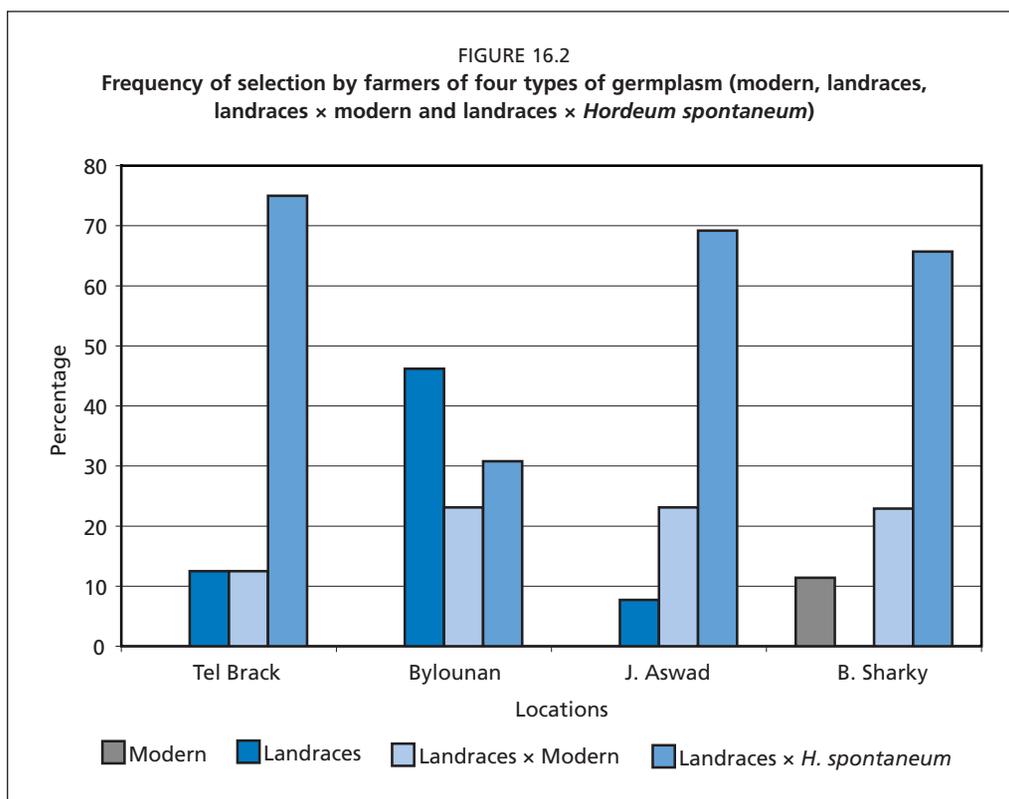


TABLE 16.3

Gas exchange parameters of *Hordeum spontaneum* accessions (means of 12 accessions) and ratio *H. spontaneum*/*H. vulgare* at Tel Hadya, Syrian Arab Republic

Parameter	Units	<i>H. spontaneum</i>	<i>H. spontaneum</i> / <i>H. vulgare</i>
Net photosynthesis	$\mu\text{mol m}^{-2} \text{s}^{-1}$	16.90 ± 0.80	1.49
Leaf conductance	$\text{mol m}^{-2} \text{s}^{-1}$	0.40 ± 0.03	3.57
Transpiration efficiency		4.35 ± 0.09	0.63
Leaf temperature	$^{\circ}\text{C}$	25.50 ± 0.36	0.85
Pre-dawn leaf water potential	Mpa	0.89 ± 0.25	1.35

higher net photosynthesis and lower pre-dawn leaf water potential at this stage of development than did cultivated barley (Table 16.3). The ability of some accessions of *H. spontaneum* to tolerate extreme levels of drought stress was evident during the severe drought of 1987, when two lines of *H. spontaneum* were the only survivors in the breeding nurseries grown at Bouider (Syrian Arab Republic), which had received

only 176 mm rainfall (Grando, von Bothmer and Ceccarelli, 2001).

These lines had some photosynthetic activity early in the morning, even though six times less than in absence of stress, stomata were open and the pre-dawn leaf water potential was negative. At the same time, the stomata of the black-seeded local landrace, Arabi Aswad, considered by farmers to be very resistant to drought,

were closed, even though the pre-dawn leaf water potential was slightly higher than in *H. spontaneum*. By midday, the stomatal conductance of *H. spontaneum* decreased and net photosynthesis became negative, while the stomatal conductance of Arabi Aswad was zero.

16.5 BREEDING METHODS

Individual plant selection (such as in the widely used 'pedigree method') in crops that are normally grown in dense stands is very effective for traits that are not affected by competition. The best example is probably disease resistance. However, many characters of interest to the breeder are strongly affected by competition. Among others, the ability to tolerate water stress is certainly greatly affected by the distance between plants competing for limited available water. The result is that isolated plants (such as those of a spaced-plant F_2 used in the pedigree method) grow much better than they would if planted at normal density. The argument that this does not matter as long as all plants are in the same conditions ignores the possible effects of genotype \times competition interaction.

One breeding method that, in the case of self-pollinated crops, seems particularly suitable to breeding for resistance to abiotic stresses is the bulk-pedigree method, in which, after producing the F_1 and the F_2 on station, three years of multilocation yield testing and selection of the bulks are carried out in the target environment(s). Selection is done between bulks by identifying the best populations for either yield or other characters. In parallel with the field testing of the bulks, a within-bulks selection is conducted only in those bulks that are selected for the next level of field testing: 10 to 50 heads are collected from the selected populations. The progenies of the selected

heads are grown as head rows and tested for disease resistance or quality characteristics. Some bulks will lose the superiority shown the year before because of genotype \times environment interaction and because of decreasing heterozygosity and associated reduced heterotic effects. The corresponding families will also be discarded.

The families deriving from the populations that maintained their superiority for three cropping seasons will enter yield testing.

When the programme is fully implemented, the yield trials contain two types of materials: new bulks, and pure lines derived from the superior bulks of the previous cycle. If the requirements for the genetic uniformity of the varieties to be released in a given country are very strict, only the pure lines will be considered as candidates for release.

The method is based on the basic assumptions that (i) a superior bulk is made by a large number of superior genotypes, and (ii) that if the superiority is maintained for a period of three cropping seasons in a highly variable environment, the probability is small that the superiority is associated with heterosis. The method can also be used to test the importance of population buffering in relation to stability.

The method is based on the exploitation of the genetic variance between populations (V_b) because estimates of V_b are comparatively easy and economical to obtain, while estimates of within-population variance (V_w) are more expensive and much less precise because of interaction and competitive effects (Simmonds, pers. comm.).

This method has proved to be ideal for use in participatory breeding programmes with self-pollinated crops (Ceccarelli and Grando, 2007).

16.6 SELECTION CRITERIA

The interest in selecting for traits other than yield in plant breeding programmes aimed at increasing crop production is motivated by the difficulties inherent in selecting directly for yield. Literature on the inheritance of yield in several crops has led to the conclusion that yield is inherited in a complex manner (Blum, 1988). In spite of the widespread reference to 'yield genes', it is evident that yield as such is not under 'direct genetic control'. Rather, it is the multitude of physiological and biochemical processes—the integrated effect of which is measured as yield—that are under genetic control (Blum, 1988). The complex manner of inheritance of yield is evident from the generally low estimates of heritability that are of common occurrence for characters that are under complex genetic control. The difficulties of selecting for yield become even greater in environments characterized by unpredictable variability in the frequency, timing and severity of a number of climatic stresses.

Breeding for drought resistance based on putative traits (defined as traits associated with drought resistance, but easier to select for than grain yield) has been, and still is, very popular (Richards *et al.*, 2002).

The ideal trait to be used as an additional or alternative selection criterion to yield in breeding for stress conditions should satisfy the following requirements: (i) be causally related or genetically linked to yield under stress conditions; (ii) exhibit genetic variation; (iii) be highly heritable; and (iv) be easy, inexpensive and quick to screen for.

Traits that have been investigated include physiological and biochemical traits (such as osmotic adjustment, proline content, stomatal conductance, epidermal conductance, cell membrane stability, cell wall rheology, canopy temperature, relative water content,

leaf turgor, abscisic acid content, transpiration efficiency, water-use efficiency, carbon isotope discrimination and re-translocation), and developmental and morphological traits (such as leaf emergence, early growth vigour, leaf area index, leaf waxiness, stomatal density, tiller development, flowering time, maturity rate, vernalization requirement and root characteristics).

In the case of barley, traits more consistently associated with higher grain yield under drought are growth habit, early growth vigour, earliness, plant height under drought, long peduncle and a short grain-filling duration (Acevedo and Ceccarelli, 1989). Three traits that deserve a special mention are leaf epidermal conductance (Sinclair, 2000), osmotic adjustment (Serraj and Sinclair, 2002) and desiccation tolerance (Ramanjulu and Bartels, 2002), which appear related to survival under severe stress conditions. Even though the low yields resulting from survival traits may look irrelevant from the perspective of high-input agriculture, they are crucial to the livelihood of farmers in some of the driest regions of the world.

While the analytical approach has been very useful in understanding which traits are associated with drought tolerance and why, it has been less useful in actually developing new cultivars showing improved drought resistance under field conditions. Under such conditions, drought varies in timing, intensity and duration, and therefore it is the interaction among traits to determine the overall crop response to the variable nature of the drought stress rather than the expression of any specific trait (Ceccarelli, Acevedo and Grando, 1991). A typical example is offered by early growth vigour, a trait that is unanimously considered important in reducing the amount of water lost by evaporation from the soil

surface, and therefore in increasing water-use efficiency (Richards *et al.*, 2002) in crops grown on current rainfall (absence of stored moisture). The study of barley landraces from the Syrian Arab Republic has revealed that genotypes with a modest early vigour can successfully achieve the same result with a prostrate growth habit (Ceccarelli and Grando, 1999).

Furthermore, many of the studies on putative traits have been conducted independently from, or as a side-activity to, breeding programmes, and by non-breeders. As a consequence, in general, breeders have taken a sceptical attitude towards these studies, with the well-founded justification that the stated conclusions are affected by either the low number of genotypes involved, or the particular type of germplasm used or the insufficient number of environments. This attitude emerges clearly even in the case of individual-trait breeding to enhance genetic yield potential (Rasmusson, 1987).

Breeding for drought resistance based on direct selection for grain yield in the target environment (empirical or pragmatic breeding) appears intuitively to be the most obvious solution. However, it has faced the major criticism that since field-drought is such a moving target, the chances of progress appear slow at best and possibly remote. One major consequence of this attitude has been to study a less mobile target by simulating drought in laboratory (or greenhouse) conditions, which results in generally irrelevant shocks (Passioura, 2002). Several studies have been and are being conducted addressing 'laboratory drought' with the main justification being to discover mechanisms and genes (Yamaguchi-Shinozaki and Shinozaki 1994; Kasuga *et al.*, 1999; Nakashima *et al.*, 2000; Seki *et al.*, 2001).

While there is currently substantial investment in molecular approaches to the study of drought resistance, there are not yet success stories based on the identification of specific genes and their utilization for this challenge (Chapman, 2008).

Ultimately it is the drought resistance under field conditions that needs to be improved. Yield under stress conditions continues to be the major selection criterion. In the case of barley, additional selection criteria utilized are early growth vigour, plant height under stress, tillering and earliness.

16.7 ARCHITECTURE OF GENOTYPES AND YIELD STABILITY

One of the most dramatic changes introduced by modern agriculture has been reduction of variability. The narrowing of the genetic base that has been a feature of plant breeding in developed countries has been accompanied by a trend towards homogeneity: one clone, one pure line, one hybrid (Simmonds, 1983). Uniformity and broad adaptation are very useful attributes to accommodate large-scale centralized seed production (Davis, 1990). While this trend is now being questioned in developed countries (Wolfe, 1992), it is still very common in breeding programmes for developing countries at both national and international levels.

In breeding programmes aiming at increased stability, the problem of reduced variability is particularly serious in relation to the two major genetic mechanisms promoting stability: individual buffering and population buffering. Individual buffering is largely a property of heterozygotes, and although there is some evidence of individual buffering not associated with heterozygosity, it may be difficult to exploit this mechanism in self-pollinated

diploid crops (Allard and Bradshaw, 1964). However, as modern varieties of cereal crops such as wheat and barley are mostly pure lines, they must rely on individual buffering to be stable. Population buffering is a mechanism of stability associated with genetic heterogeneity. 'Varieties' made up of a number of genotypes, such as the landraces, are well buffered (stable), because each member of the population is best adapted to slightly different conditions from other members of the population. The stability of the individuals is sacrificed to maximize the stability of the population. Although a direct relationship between genetic heterogeneity and stability has yet to be demonstrated for landraces, it can be speculated that, being the product of natural and artificial selection following domestication, the genetic structure of landraces must bear some advantage, or at least cannot be a purely random outcome.

The genetic structure of landraces, therefore, may be considered an evolutionary approach to survival and performance under arid and semi-arid conditions (Schulze, 1988). It follows

that, during millennia of cultivation under adverse conditions, natural and artificial selection have not been able to identify either an individual genotype possessing a key trait associated with its superior performance, or an individual genotype with a specific architecture of different traits. On the contrary, the combined effects of natural and artificial selection has led to diversity in architecture of genotypes, representing different combinations of traits. These populations can be extremely useful for understanding mechanisms that enhance stability in stress environments, not only from the genetic structure point of view, but also for understanding the adaptive role of given traits. In fact, although variable, landraces grown in environments characterized by a high frequency of stress conditions tend to present a high frequency of a given expression of specific traits.

For example, barley lines extracted from landraces collected from five sites in the Syrian steppe (Table 16.4) were compared with barley lines extracted from landraces collected in Jordan and with a wide range of

TABLE 16.4

Mean of morphological and developmental traits in 1041 modern barley genotypes (unrelated to Syrian or Jordanian landraces) compared with 322 pure lines extracted from Syrian landraces and 232 pure lines from Jordanian landraces

Traits	Modern (n=1041)	Landraces	
		Syrian Arab Republic (n=322)	Jordan (n=232)
1. Early growth vigour	2.5 b	3.2 a	2.4 b
2. Growth habit	2.8 c	4.0 a	3.1 b
3. Cold tolerance	3.0 a	1.3 c	2.3 b
4. Days to heading	117.9 b	121.2 a	116.9 c
5. Grain filling	39.3 a	35.5 c	37.4 b
6. YP (t/ha)	4.398 a	3.293 c	3.947 b
7. YD (t/ha)	0.483 c	0.984 a	0.835 b

Notes: (i) Traits 1, 2, 4, 5 & 6 were scored or measured at Tel Hadya in 1987/88 (504.2 mm rainfall); trait 3 was scored at Bouider in 1987/88 (385.7 mm rainfall); and trait 7 was measured at Bouider in 1988/89 (189 mm rainfall), on 521 modern lines, 92 Syrian landraces, and 86 Jordanian landraces. Early growth vigour (1=good; 5=poor), Growth habit (1=erect; 5=prostrate), Days to heading (days from emergence to awn appearance), Grain filling duration (days between heading and maturity), YP = Yield Potential, YD = Yield under Drought.

(ii) Means followed by the same letter are not significantly ($P < 0.05$) different based on t-test for samples of unequal size.

modern (non-landrace) barley genotypes. The Syrian lines showed a higher frequency of genotypes with prostrate or semi-prostrate growth habit, cold tolerance and short grain-filling period, and a lower frequency of genotypes with good growth vigour and early heading. Their average grain yield in unfavourable conditions (at Bouider in 1989) was 0.984 t/ha (ranging from 0.581 to 1.394 t/ha), more than twice the average grain yield of modern genotypes (0.483 t/ha, ranging from crop failure to 1.193 t/ha). The average yield in favourable conditions of the Syrian landraces (3.293 t/ha) was 75 percent of the average yield in favourable conditions of the modern germplasm (4.398 t/ha).

Although this particular set of data is based on one environment only, it confirms the existence of the trade-off between yield in unfavourable conditions and yield in favourable conditions discussed earlier. Landraces collected in Jordan, from sites with milder winters than the Syrian steppe, have a higher frequency of genotypes that have better early growth vigour, more erect habit, less cold tolerance, slightly longer grain-filling period and earlier heading than Syrian landraces. Their average grain yield in unfavourable conditions was only slightly lower (0.835 t/ha) than Syrian landraces, while their average yield in favourable conditions (3.947 t/ha) was in between the Syrian landraces and the modern germplasm. Syrian landraces therefore show a combination of escape (early maturity) and avoidance (prostrate habit and cold tolerance result in good ground cover) mechanisms.

In addition to the high frequency of combinations of escape and avoidance traits, landraces possess another powerful mechanism. They are composed of a number of genotypes with a variable expression for

each of these traits. The variability around a mean expression of each character—which already allows a high degree of adaptation—might perhaps be considered as a fine-tuning mechanism to cope with environmental fluctuations. Thus, 321 lines derived from Syrian landraces were classified according to the score for early growth vigour in three classes: good vigour (score <2.5); intermediate (score = 2.5–3.5); and poor vigour (score >3.5). Each class was then classified according to the score for growth habit (erect <2.5; semi-prostrate = 2.5–3.5; prostrate >3.5). No genotypes were found in the good vigour-erect, intermediate vigour-erect, poor vigour-erect, and poor vigour-semi-prostrate classes (Table 16.5).

The groups were compared not only for the two traits used in their classification, but also for days to heading, cold tolerance and length of the grain-filling period. Lines with good early growth vigour tend to be less cold tolerant, earlier and with a longer grain-filling period. This small percentage of genotypes will presumably have a yield advantage in years with slightly milder winter temperatures, absence of late frosts and less severe terminal stress. The highest frequency of genotypes (71.3 percent) combines intermediate early-growth vigour with semi-prostrate or prostrate growth habit. These genotypes are slightly more cold tolerant than the first group, but are slightly later in heading. However, they are better equipped to escape terminal drought because of the shorter grain-filling period. About one-quarter of the genotypes (22.1 percent) have poor early growth vigour but a very prostrate growth habit (growth habit score = 4.2) and a high level of cold tolerance (1.3). Their slightly, although significantly, later heading is not necessarily a negative attribute, mostly because it is compensated for by a very

TABLE 16.5

Frequency of different combinations of early growth vigor (GV), and growth habit (GH), and mean values of cold tolerance (CT), days to heading (DH) and length of the grain filling period (GF) in a sample of 322 lines of barley collected in the dry areas of the Syrian Arab Republic (from same trials as indicated in notes of Table 16.4)

Groups	%	GV	GH	CT	DH	GF
1. Good vigour–Erect	0.0	-	-	-	-	-
2. Good vigour–Semiprostrate	1.2	2.2	3.3	1.6	118.8	37.4
3. Good vigour–Prostrate	5.3	2.4	3.9	1.4	119.8	36.6
4. Intermediate vigour–Erect	0.0	-	-	-	-	-
5. Intermediate vigour–Semiprostrate	6.2	2.9	3.4	1.5	119.7	35.8
6. Intermediate vigour–Prostrate	65.1	3.1	4.0	1.4	121.2	35.4
7. Poor vigour–Erect	0.0	-	-	-	-	-
8. Poor vigour–Semiprostrate	22.1	3.9	4.2	1.3	121.9	35.4
9. Poor vigour–Prostrate	22.1	3.9	4.2	1.3	121.9	35.4
Least Significant Difference – LSD _{0.05}		0.2	0.1	0.1	0.6	0.7

Notes: All collection sites are included in the Palmyra region, as defined by Weltzien (1988).

short grain-filling period. In an environment characterized by a combination of different abiotic stresses with varying intensity and frequency every year, a population with such architecture of genotypes is probably the best solution to long-term stability (Ceccarelli, Acevedo and Grando, 1991).

The evidence that, at least in the short term, some individual genotypes (pure lines) are able to show the same degree of stability as local heterogeneous populations has been presented earlier (the examples of cvs. Tadmor and Arta). Even so, the use of population buffering in addition to individual buffering offers scope for further increased stability.

In conclusion, the evidence discussed suggests that:

- genetic differences in yield and yield stability under conditions of low winter temperatures and moisture stress are associated with differences, among others, in morphological and developmental traits such as growth habit, cold tolerance, growth vigour and time to flowering. In other types of stress environments and/or in other crops the suite of traits will obviously be different;

- it is the interaction among these, and possibly other traits, that plays a key role in determining the differences in overall performance rather than the expression of any one of them taken in isolation;
- because of the interactions among traits, different combinations of traits are expected to produce the same effect in terms of final yield;
- the role of each individual trait, even within the restricted terms of reference that have been chosen, depends on the frequency, timing and severity of stresses, and on the type of stress; therefore, efforts to identify individual traits causally associated with yield stability under stress are unlikely to be successful;
- in this type of stress environment, ‘drought resistance’, defined in terms of yield under stress, is a genetic abstraction as much as yield in general;
- analytical breeding to enhance yield stability in stress environments has to consider individual traits as part of an architecture, rather than in isolation; and
- long-term and sustainable improvements of yield stability should probably

be based on population buffering as achievable with mixtures of genotypes representing different, but equally successful, combinations of traits, as occurs in landraces.

16.8 PLOT TECHNIQUES AND EXPERIMENTAL DESIGNS

When genotypes are compared at increasing levels of moisture stress, small variations in soil depth, texture and topography have increasingly large effects on plot-to-plot variability because of associated differences in soil moisture availability. Therefore, it becomes essential to adopt plot techniques and experimental designs that can minimize these effects.

Various plot techniques to increase the efficiency of direct selection in the presence of abiotic stresses have been discussed extensively in Chapter 3 of this volume.

16.9 DECENTRALIZED-PARTICIPATORY SELECTION

The term 'decentralized selection' was first used by Simmonds (1984) and defined as selection in the target environment(s). Decentralized selection becomes selection for specific adaptation when the selection criterion is the performance in specific environments rather than the mean performance across environments. Selection for mean performance across a number of environments (years and locations) tends to exclude breeding material that performs very well in the lowest yielding years or locations but not particularly well in the highest yielding years or locations, unless data are standardized. On the contrary, selection for the highest yielding breeding material in specific locations or areas will automatically include breeding material performing well across all locations. In other words, selection for specific spatial adaptation will

not exclude breeding material with wide spatial adaptation, while selection for wide adaptation tends to eliminate breeding material with specific adaptation.

Decentralized selection is different from decentralized testing, which is a common feature of breeding programmes and takes place, usually in the form of multilocation trials and on-farm trials, after a number of cycles of selection in one or few environments (usually with high levels of inputs).

Decentralized breeding is a powerful means to adapt crops to the physical environment. However, to exploit fully the potential gains from specific adaptation to low-input conditions, breeding must be decentralized from research stations to farmers' fields. Although decentralization and farmer participation are unrelated concepts, decentralization to farmers' fields almost inevitably leads to the participation of farmers in the selection process (Ceccarelli and Grando, 2002).

16.10 DECENTRALIZED-PARTICIPATORY PLANT BREEDING

The implementation of decentralized-participatory plant breeding (PPB) programmes started in 1997 with the aim of developing an alternative way of conducting plant breeding that is much more efficient and much quicker in bringing new varieties to farmers, and ensures that the new varieties are adapted to farmers' specific environments and end-uses.

The emphasis of the programme has been on dry areas, even though the approach can also be beneficial to high-rainfall environments.

The programme, which has been described in detail by Ceccarelli and Grando (2007) and by Ceccarelli, Grando and Baum, (2007), is based on the following concepts:

- the trials are grown in farmers' fields using the host farmer's agronomic practices;
- selection is conducted by farmers in farmers' fields, so that farmers are the key decision-makers; and
- the traditional linear sequence of Scientist → Extension → Farmers is replaced by a team approach, with Scientists, Extension Staff and Farmers participating in all major steps of variety development (see Figure 9.1).

In a conventional breeding programme, the most promising lines are released as varieties, their seed is produced under controlled conditions (certified seed) and only then can farmers decide whether to adopt them or not. In many developing countries the process results in many varieties being released but only a small fraction being adopted. The major consequence of the PPB concept is that the process transforms the delivery phase of a plant breeding programme from being supply driven to being demand driven.

Under PPB, it is the initial farmers' preference that drives the decision of which variety to release. As a consequence, adoption rates are higher, and risks are minimized, as intimate knowledge of varietal performance

is gained as part of the selection process. Last, but not least, the public investment in seed production is nearly always paid off by farmers' adoption.

The programme started in the Syrian Arab Republic in 1996 and was expanded to Algeria, Egypt, Eritrea, Islamic Republic of Iran, Jordan, Morocco, Tunisia and Yemen, using the same bulk-pedigree method described earlier. Four types of impact can be observed, considered below.

Variety development

New varieties were spontaneously disseminated from farmer to farmer as early as three years after starting the programme. In the Syrian Arab Republic, several thousand hectares are planted with two varieties, and 12 varieties have been adopted by farmers and are under seed multiplication (Table 16.6). Varieties are adopted both in dry areas and in wetter areas in a much shorter time than in a conventional breeding programme. It also confirms the importance of landraces (Tadmor, Arta, SLB and JLB lines, Zanbaka, A. Abiad and A. Aswad) as well as *H. spontaneum* when farmers' opinion becomes part of the breeding process.

TABLE 16.6

Varieties adopted from the PPB programme by farmers in the Syrian Arab Republic

Pedigree	Name	Location	Rainfall
H.spont.41-1/Tadmor	Raqqa-1	Bylounan	212.4
Arta/H.spont.41-5/Tadmor	Raqqa-2	Bylounan	212.4
Zanbaka/JLB37-064	Karim	Bylounan	212.4
Tadmor/3/Moroc9-75/ArabiAswad/H.spont.41-4	Akram	Bylounan	212.4
Mo.B1337/WI2291//Moroc9-75/3/SLB31-24	Suran-1	Suran	383.7
ChiCm/An57//Albert/3/Alger/Ceres.362-1-1/4/Arta	Suran-2	Suran	383.7
ER/Apm//Lignee131/3/Lignee131/ArabiAbiad/4/Arta	Suran-3	Suran	383.7
Hml-02/5/./Alger/Ceres362-1-1/4/Hml	Nawair-1	Suran	383.7
Hml-02/5/./Giza 134-2L/6/Tadmor	Nawair-2	Suran	383.7
SLB03-10/Zanbaka	Yazem	J. Aswad	226.4
Tadmor//Roho/Mazurka/3/Tadmor	Salam	J. Aswad	226.4
ArabiAswad/WI2269/3/ArabiAbiad/WI2291//Tadmor /4/Akrash//WI2291/WI2269	Ethiad	J. Aswad	226.4

Note. Rainfall is annual rainfall in mm, average of the period 2000–2005.

Institutional

In several countries, PPB has generated considerable change in the attitude of policy-makers and scientists towards the benefits of participatory research, and generated changes in national breeding programmes.

Farmers' skills and empowerment

The cyclic nature of the PPB programmes has considerably enriched farmers' knowledge, improved their negotiation capability, and enhanced their self esteem. By the same token, scientists (breeders) have been enriched by the farmers' indigenous knowledge of the crops they grow and the environments in which they grow them.

Enhancement of biodiversity

Different varieties have been selected in different areas within the same country, and

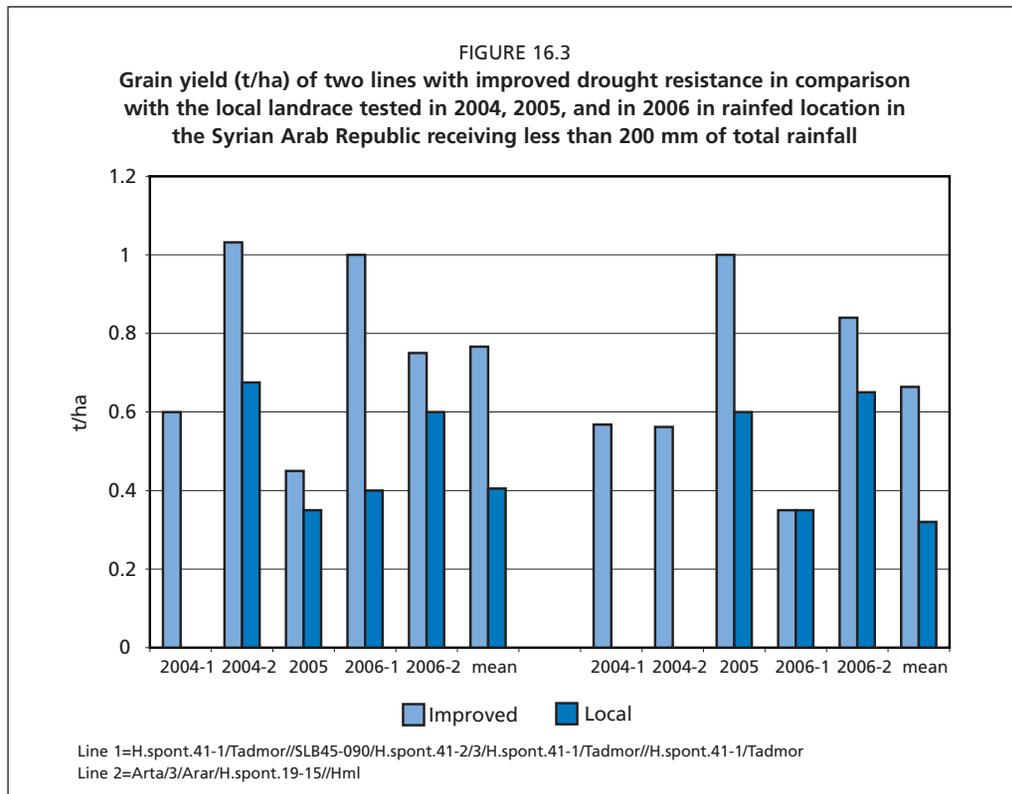
even within the same location (as shown in Table 16.6) in response to different environmental constraints and users' needs.

16.11 DROUGHT-RESISTANT LINES

PPB was not specifically designed to breed for drought tolerance, but rather to adapt the crops to a number of environmental and agronomic conditions and to farmer preferences. These also include situations where drought stress occurs frequently and can be very severe. Therefore it is not surprising that the PPB programme has produced the breeding material with the highest level of drought tolerance.

In this section we will give two examples of lines specifically adapted to dry areas.

The first example refers to lines selected in the Syrian Arab Republic in 2000, when the total rainfall in most areas of the country was



below average and crop yields were severely affected. In some areas, the rainfall was so low that the crop did not even germinate; in many others the crop failed to produce grain. The PPB trials, planted in eight farmers' fields in the Syrian Arab Republic, were affected by different intensities of drought. At one extreme, the rainfall was only 50 mm in the entire season and no germination occurred. At the other extreme, the rainfall was 252 mm rainfall and average grain yield was 1.8 t/ha (ranging from 1.0 to 3.2 t/ha). The driest sites, where some new barley entries were able to produce some grain or some biomass, received between 87 and 130 mm. Average grain and biomass yield were very low but some lines were able to produce between 0.3 and 0.5 t/ha of grain

and between 0.5 and 3.0 t/ha of biomass yield (Ceccarelli *et al.*, 2004).

Two of these lines were tested by farmers on large areas (5–20 ha) in 2004, 2005 and 2006, which were all very dry (Figure 16.3). In comparison with the local landrace, which itself is considered to be drought resistant, the two lines showed an average yield advantage of 44 percent, ranging from 9 percent to 67 percent. This includes one case in which the local landrace failed, and one of the improved lines yielded 0.5 t/ha. Both lines are derived from crosses with a pure line of *H. spontaneum* (the wild progenitor of cultivated barley), an indication that some *H. spontaneum* lines can contribute significantly to enhance the drought resistance of cultivated barley.

TABLE 16.7

Rainfall (mm) and average yield (in parenthesis in t/ha) in five locations in the dry areas of the Syrian Arab Republic during the three years 2003–2005

Location	No. of lines	2003	2004	2005	Mean annual rainfall 2000–2005 (mm)
Bylounan	8	187 (1.249)	217.4 (0.804)	196 (0.604)	212.4
J. Aswad	6	215 (1.152)	245.3 (0.808)	238 (0.853)	226.4
Melabya	10	275.9 (1.496)	176 (0.432)	187.5 (0.466)	186.5
Siebatt	12	308 (1.406)	319 (0.478)	263 (1.027)	248.8
Al Bab	10	408 (1.355)	296 (0.422)	289.5 (1.084)	307.5

TABLE 16.8

Grain yield (as percentage of the local check) of the highest yielding lines during 2003, 2004 and 2005 in five dry locations in the northern Syrian Arab Republic receiving between 186 and 308 mm total annual rainfall

Location	Line	2003	2004	2005	Mean
Bylounan	Arta/SLB22-74	1.109	1.030	1.065	1.068
Bylounan	ArabiAbiad/Arar//H.spont.41Arta/.....	1.087	1.100	0.993	1.060
Bylounan	Arta//H.spont.41-5/Tadmor/3/SLB05-096	1.098	1.102	0.982	1.060
J. Aswad	SLB28-53/SLB21-81	1.030	1.121	0.967	1.039
Melabya	Roho/4/Zanbaka/3/ER/Apm//Lignee131	1.151	1.045	1.071	1.089
Melabya	ArabiAbiad/Arar//H.spont.41Arta/.....	0.957	1.038	1.101	1.032
Siebatt	SLB21-81/SLB22-74	1.216	1.085	1.023	1.108
Siebatt	Anadolu86/Sara-02//Zanbaka	1.186	0.993	1.128	1.102
Siebatt	Zanbaka/SLB21-81	1.180	1.038	1.036	1.084
Siebatt	Sara-01/Sara	1.433	1.009	0.998	1.147
Al Bab	ChiCm/An57//Albert/3/Alger/Ceres.362	1.323	1.535	1.207	1.355
Al Bab	SLB28-53/SLB21-81	1.282	1.472	1.300	1.352

The second example derives from trials conducted in dry locations in the northern Syrian Arab Republic during the period 2003–2005. Two locations (Bylounan and Melabya) represent some of the driest areas in the Syrian Arab Republic, where barley is the only possible rainfed crop; J. Aswad and Siebatt are in slightly wetter areas, while Al Bab is a location characterized by colder winters than the other four. In the two driest locations, rainfall varied from 176 mm to 245.3 mm total annual rainfall and average grain yield from 0.432 to 1.496 t/ha during the testing period. In the two wetter locations, rainfall varied from 215 to 319 mm total annual rainfall and average grain yield from 0.478 to 1.406 t/ha, while Al Bab was the wettest of the five locations but not the highest yielding because of the low temperatures in winter (Table 16.7).

In the five locations, we tested between 6 and 12 lines (including the checks) representing the result of two cycles of decentralized participatory selection starting from a common set of 165 lines. The yield of the best lines is shown in Table 16.8, expressed as a percentage of the local check.

At the two driest sites, Bylounan and Melabya, five lines outyielded the local check on average over 3 years by between 3.2 percent and nearly 9 percent, but only three lines were consistently superior to the local check in each of the three years. In the two wetter locations, five lines outyielded the local check by between 7.5 percent and 14.7 percent, but only the two lines in J. Aswad and two of the four lines in Siebatt consistently outyielded the local check. In Al Bab, two lines consistently outyielded the local check by slightly more than 35 percent; two lines (ArabiAbiad/Arar//H.spont.41 and SLB28-53/SLB21-81) were among the highest yielding lines in two locations (Bylounan and Melabya the

first and Al Bab and J. Aswad the second). As these lines are the product of one cycle of selection, further progress is expected with additional cycles of recombination and selection.

16.12 CONCLUDING REMARKS

The objective of this chapter has been to discuss what plant breeders can do when the target environment of their breeding programme is characterized by chronic low yields due to numerous factors, such as climatic, nutritional and abiotic stresses. The data are mostly derived from barley and from one type of dry area (dry Mediterranean with cold winters and hot summers, and crops grown on current rainfall). However, the paper illustrates some general concepts that, with some modifications, could be useful in other crops and in other types of dry area.

The first concept is that in these environments, climatic, nutritional and biotic stresses usually occur together (though not necessarily all of them all of the time); and, so far, there is little substitute for actually exposing the breeding material to a real field situation. Although little practiced, the idea is not new. Nearly forty years ago Hurd (1971) published a paper with the title: Can We Breed for Drought Resistance? The first sentence of the paper was “My answer to the above very pertinent question is a confident and optimistic ‘Yes’”. He concluded: “One method is to grow large populations in early generations under typical dry growing conditions.” Twenty years later, Bramel-Cox *et al.*, (1991) recognized that the key to increased production with fewer external inputs would be through a re-evaluation of the identification and use of selection and testing environments.

Although this concept is obvious to

many and not new, selection for stress environments is still seldom done in the target environments and it still a highly controversial issue, as it is the relationship between high yield under optimum conditions and high yield under abiotic stress conditions (see, for example, Chapter 18 in this volume). This may not always be necessarily a deliberate choice of one breeding strategy or another, but is simply due to the distance of suitable selection sites from main cities, with all the associated inconveniences. We hypothesize that in these cases an interesting solution may be offered by farmers' participation in breeding (Ceccarelli and Grando, 1997; Ceccarelli, Grando and Baum, 2007). Conducting selection in farmer's fields has the advantage of exploiting genetic differences under farm conditions, with the additional advantage of making use of the farmer's knowledge of the crop.

The second concept is the use of germplasm usually ignored by most plant breeders, such as landraces and wild relatives. This approach is a direct consequence of choosing to work in the target environment and has led to the development of a number of barley cultivars, now grown in a number of farmers' fields in the central and northern Syrian Arab Republic and in environments considered too difficult and therefore beyond the plant breeder's domain.

The third concept is that in dry areas, every effort should be made to control environmental variability in trial and nurseries evaluation. When working at stress sites, the breeder should forget the typical research-station style of work. The methodology, experiment designs and plot techniques used in the very homogeneous environment of the experiment station are not suitable; in fact, when the conclusion is reached that progress cannot be made in a

stress environment, it is probably for that reason.

The main conclusion of this paper is that breeding for stress environments is possible, provided it is conducted with strategies and methodologies that little have in common with those used in breeding for favourable environments. Adaptation over time can be improved by breeding for specific adaptation to a given type of stress environment. This can be achieved by taking advantage of the temporal variability of stress environments, which permits exposure of the same breeding material to variable combinations of stresses over a (relatively) short period and to accumulate favourable alleles at the several loci involved in drought resistance through successive cycles of recombination and selection. We are aware that this is fundamentally different from the modern trend of plant breeding towards broad adaptation over space. The difference represents the contrasting interests of farmers and seed companies. Farmers are interested in cultivars that are consistently superior on their farm, regardless of how they perform at other locations or in other countries. Seed companies, however, want to market as much seed of as few cultivars as possible. Breeders have been breeding, perhaps unconsciously, more for seed companies and for their personal prestige than for farmers. The two objectives coincide when selection and target environments are similar, but this approach has by-passed millions of small farmers in difficult environments.

Recent advances in plant genomics have enabled one to dissect various molecular mechanisms (signal transduction pathways) involved in drought, cold and salt stress tolerance and in identifying various genes involved in such stress tolerance. Information generated in genomics should

be integrated into practical plant breeding. Various genes identified, in both model plants and crop plants, could be used in future for developing stress-tolerant plants through either marker-assisted selection or direct gene transfer.

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