Expl. Agric. (2007), volume 43, pp. 411–435 © *2007 Cambridge University Press*
doi:10.1017/S0014479707005327 *Printed in the United Kingdom*

PARTICIPATORY PLANT BREEDING IN WATER-LIMITED ENVIRONMENTS

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(*Accepted 1 March 2007*)

SUMMARY

Drought is one of the major factors limiting crop production worldwide. Dry areas are a much less homogeneous population of target environments than areas with high and reliable rainfall. In this paper we argue that a decentralized participatory plant breeding programme can address the complexity of dry areas, characterized by high and repeatable genotype × locations and genotype × years within locations interactions, more efficiently and effectively than a centralized non-participatory plant breeding programme. This is because varieties can be tailored not only to the multitude of target environments typical of dry areas, but also to diverse clients needs. In addition, varieties can be delivered in a shorter time and with a higher probability of adoption. Decentralized participatory plant breeding also has beneficial effects on biodiversity because selection is for specific adaptation rather than for broad spatial adaptation. The paper gives examples of methodological aspects including the modes of farmer selection, the precision of the trials, the efficiency of selection, the response to selection, the role of the type of germplasm and the role of molecular breeding in a participatory breeding programme. The paper gives the example of drought-resistant barley lines identified through extensive field testing and selection in a decentralized participatory breeding programme, and concludes that this type of plant breeding may be better targeted, more relevant and more appropriate for poor farmers in marginal areas.

INTRODUCTION

Drought, defined in an agricultural context as an environmental event during which water availability is below what is required for the full expression of yield potential, is one of the major factors limiting agricultural production. Rainfall and its distribution are the main factors determining drought and together with other weather variables are the main components of the various indices (such as the Standardized Precipitation Index, the Palmer Drought Severity Index, the Crop Moisture Index) (www.plantstress.com) used to measure drought.

It is commonly recognized that drought is a very complex phenomenon (Reynolds *et al*., 2005) because: i) it may occur at different times during crop growth and more than once in the same cropping season; ii) it may last a variable length of time; iii) it seldom occurs in isolation from other stresses, either abiotic (such as temperature extremes) or biotic (such as pests and diseases) (Ceccarelli *et al*., 2004); iv) it interacts with soil type and agronomic management (Sadras and Angus, 2006) and v) it affects poor farmers more than rich farmers.

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It is perhaps because of its complexity that drought means different things to different people in different areas and for different crops (Passioura, 2006). In areas where moisture is usually non-limiting, drought is often an abnormal event, which has serious consequences that do not usually extend into the subsequent seasons. In other areas, where available moisture is usually the main limiting factor, drought simply makes the situation worse. These different meanings are evident in the literature, where there are often descriptions of drought stress that differ from what many farmers experience in developing countries and in some developed countries, such as Australia. An example is given by Rizza *et al.* (2004), where in the most stressed environment barley yielded on average nearly 3 t ha^{-1}, a yield that in the Near East and in Australia is typical of a wet environment.

In countries where the agricultural area spreads across a rainfall gradient with associated different probabilities of drought events, farmers cope with differences in available moisture by growing different crops in different rainfall zones, unless they have access to irrigation water. For example, in several Mediterranean environments, wheat and chickpea are usually grown in wetter environments than barley and lentil respectively. In subtropical environments, maize, sorghum and pearl millet are grown at progressively decreasing levels of rainfall. In areas with an erratic start to the rainy season, farmers plant different crops depending on the timing of the start of the rains. This is, for example, the case in Eritrea where a suite of crops such as sorghum, pearl millet, finger millet, teff and barley are available to farmers. Eritrea and the northern part of Ethiopia also provide examples of how innovative farmers can be in developing strategies to cope with drought. In this area it is very common to find *hanfets* (a Tigrigna word for any product with different racial backgrounds), a mixture of barley and wheat which is grown with the expectation that wet years will exploit the higher yield potential of wheat while dry years will exploit the better drought tolerance of barley (Woldeamlak, 2001). In other areas, such as those with a Mediterranean climate, the combination of low rainfall and low temperatures during the wet season limits the choice of crops to only one.

An example of the variability in the amount of rainfall and its consequences on the level of drought faced by a typical rainfed crop such as barley is shown in Figure 1. The total annual rainfall in five villages in Syria between 2000 and 2005 varied from a minimum of 50 mm in village 7 in 2000 to a maximum of 539 mm in village 9 in 2004.

Within the same village the year-to-year variation is also high, with the wettest year in each village receiving from 1.8 to more than 5 times more rainfall than the driest year. As a consequence yields are also variable (Figure 2), but they seldom exceed 2.5 t ha^{-1} in the driest villages. Even in the wettest of the five villages (village 9) yields exceed 4 t ha^{-1} only exceptionally. Average yields in the driest villages are seldom more than 1 t ha^{-1} and in the wettest village are about 3 t ha^{-1}. The data reported in Figures 1 and 2 also underline the importance of rainfall distribution and other weather variables; in fact, the value of R^2 of grain yield on rainfall varied from 0.11 to 0.75.

Different definitions of drought are one of the causes of the controversy about how to deal with a multitude of target environments (Cooper, 1999) which divides plant

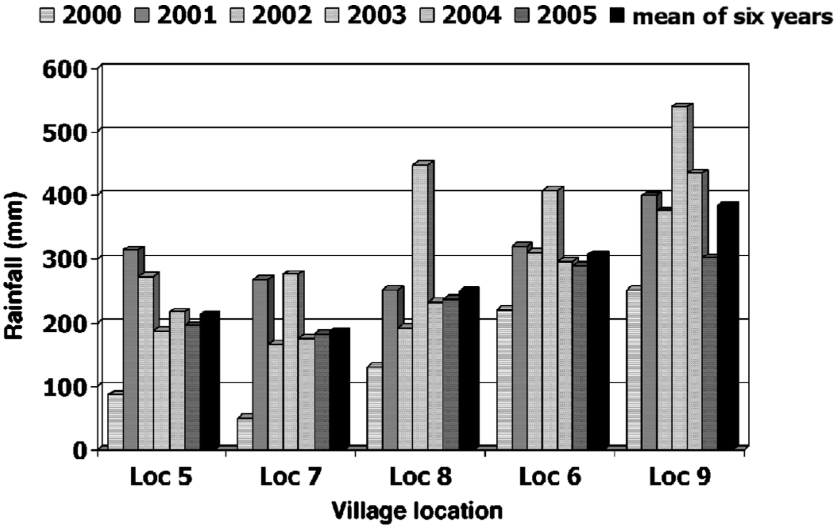

Figure 1. Total annual rainfall (mm) in five villages in Syria over six years and mean across years representing the most extreme of the 23 villages where the participatory barley breeding programme was implemented.

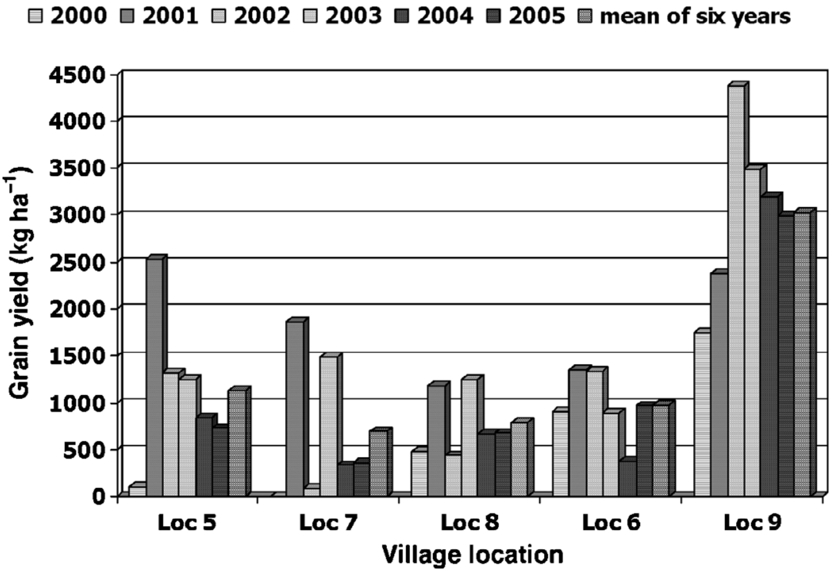

Figure 2. Average grain yield (kg ha^{-1}) in five villages in Syria over six years and mean yield across years representing the most extreme of the 23 villages where the participatory barley breeding programme was implemented.

breeders between those in favour of broad adaptation and those in favour of specific adaptation. In addition to defining as dry a year or a location that in other contexts is actually favourable, the issue of broad and specific adaptation is often discussed using data collected from a narrow range of environments. Two examples are two-row barley in Canada (Atlin *et al.*, 2000), where the ratio between the highest yielding environment and the lowest (nearly 3 t ha^{-1}) was 1.8, and where, not surprisingly, no crossover interaction (change of ranking of varieties in different environments) was found, and winter wheat in France, where the average yields of the two most extreme environments were 5.9 (dry) and 9.5 t ha^{-1} (Brancourt-Hulmel *et al.*, 2003).

One problem in breeding for drought resistance is that genotype × location (GL) interactions tend to be higher in dry than wet locations. This can be shown through biplots, which are constructed using the first two principal components (PC1 and PC2) derived by subjecting a two-way (genotypes and environments) matrix, with or without transformation, to singular value decomposition (Yan, 2000); the biplot displays the environments (locations and/or years) as vectors drawn from a common origin ($PC1 = PC2 = 0$), and the genotypes as points. Similar environments have a small angle (the angle formed between the first vector, the origin and the second vector) between them while dissimilar environments have a large angle between them; similar genotypes have a small angle while dissimilar genotypes have a large angle (the angle formed between the first genotype, the origin and the second genotype). Genotypes far from the origin (e.g. Rihane-03 in Figure 4a) have a large genotype plus interaction effect. If a given genotype and a given environment vector are on the same side of the origin (e.g. Rihane-03 and BR_96 in Figure 4a) that genotype performs above average in that environment. By contrast, a genotype which is at the opposite side of an environment vector origin (example Rihane-03 and BO_98 in Figure 4a) performs below average in that environment. Eventually genotypes close to the origin (Arta and Harmal in Figure 4b) have an average performance in all environments (Yan *et al.*, 2000).

The biplot in Figure 3 is based on 200 genotypes grown in nine villages and two research stations (Ceccarelli *et al.*, 2000) and shows that the yields in three villages in high rainfall areas (IB, SU and EB) are highly correlated among themselves and are highly correlated with a research station (TH) situated in the same rainfall zone. By contrast, yields in villages located in dry areas are poorly correlated among themselves and only few are positively correlated with those on the research station located in a dry area (BR).

An additional complication is that genotype × years within location interactions tend to be higher in locations in dry areas than in locations with high rainfall. The biplots in Figure 4 refer to a common set of seven varieties grown in two locations in dry areas (average yield = 1.3 t ha^{-1}) and in two locations in high rainfall areas (average yield = 3.5 t ha^{-1}) for four years (1995 to 1998).

Genotype × environment interactions (including both genotype × locations and genotype × years) are nearly 90 % in locations in the dry areas while they are slightly less than 50 % in the two locations in high rainfall areas. In addition, the genotype × years within locations interactions are much larger in the locations in the dry areas as indicated by the spreading of the vectors associated with the four years within the same location. In this situation it is nearly impossible to identify a common winner across years and across locations. By contrast, the genotype × years within locations interactions are much smaller in the high rainfall locations, where it is easier to identify a common winner (such as the variety Rihane-03) across years and locations.

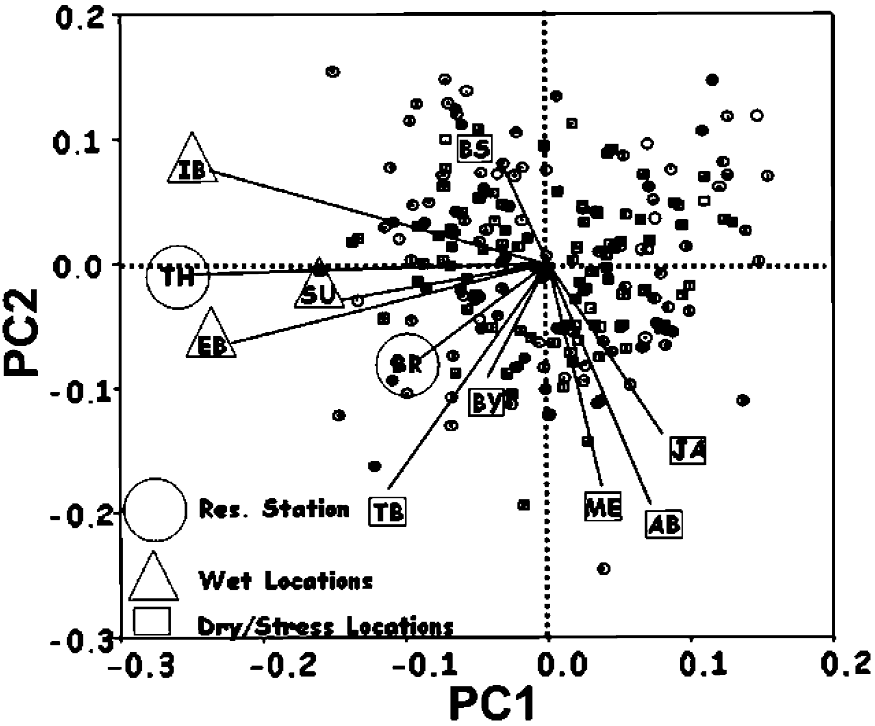

Figure 3. Biplot of grain yields of 200 barley genotypes in nine villages, three in high rainfall (IB, SU, EB) and six in low rainfall (BS, TB, BY, ME, AB, JA) areas and in two research stations (TH and BR), representing high and low rainfall areas, respectively.

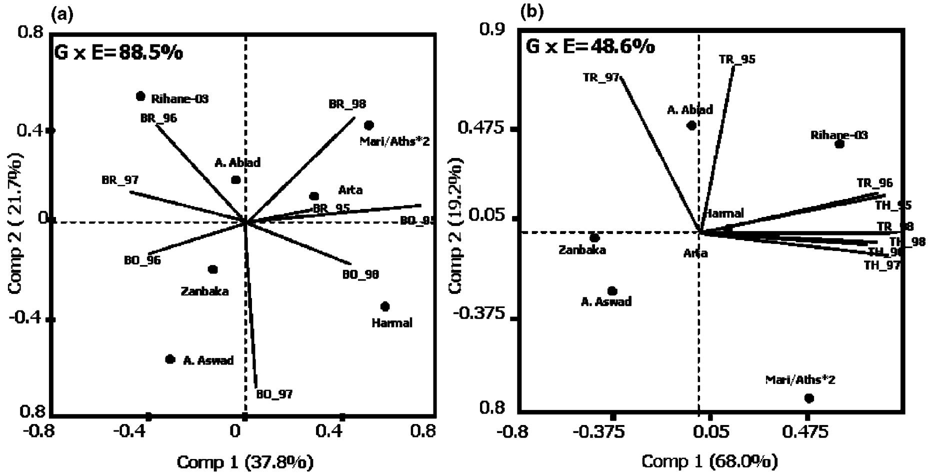

Figure 4. Total genotype × environment and genotype × years interactions within locations in the case of seven varieties grown in two dry locations (a) and in two high rainfall locations (b) for four years. (BR: Breda; BO: Bouider; TH: Tel Hadya; TR: Terbol) (from Ceccarelli and Grando, 2007).

The biplots in Figure 4 explain why plant breeding for dry areas is much more difficult than for high rainfall areas and why progress has been much less satisfactory. This is due to the variation in occurrence, timing, intensity and duration with which drought occurs in field conditions, and to its interactions with other abiotic stresses (mainly temperature), biotic stresses and management factors.

Figure 4 also indicates the difficulty of simulating the complexity of drought in the real world by either managing drought environments or by experiments in a controlled environment. With reference to Figure 4: which type of drought should we simulate, BR97 with 1002 kg ha^{-1} or BR95 with 746 kg ha^{-1}, two dry years within the same location which discriminated among genotypes in a highly contrasting way?

The picture emerging from the data presented so far is of a much larger complexity in low rainfall than in high rainfall areas, suggesting the need for a wider diversity of varieties (Bellon, 2006). This is associated with the observation that, under field conditions, drought may occur in a multitude of ways even if the final product, i.e. low yield, is the same.

The main objective of this paper is to test the hypothesis that in order to address efficiently and effectively the complexity of low rainfall areas a different type of plant breeding process may be more appropriate. This is decentralized participatory plant breeding, which emphasizes the development of varieties specifically adapted to a multitude of target environments defined according to the repeatability of genotype × locations interactions (Annicchiarico, 2002; Annicchiarico *et al.*, 2005; Singh *et al.*, 2006), unlike conventional practices that address reliable environments by breeding for broad adaptation. By emphasizing specific adaptation, participatory plant breeding is also expected to be more capable than conventional plant breeding of addressing some of the specific problems which are common to many conventional breeding programmes in developing countries. According to Bellon (2006) and Ceccarelli *et al.* (1996; 1997; 2000) these include:

- limited success in the majority of marginal environments
- length of time needed to release varieties and an even longer period for the varieties to reach the farmers
- mismatch between the varieties which are officially released and those which are grown by farmers: a large number of varieties are released, but few are adopted by farmers and, on the other hand, farmers often grow varieties which have not been released officially or have been rejected by the official system
- seed availability and price for those officially released varieties which are acceptable to farmers
- reduction of biodiversity.

Before introducing the model of participatory plant breeding which was developed between 1996 and 2004 to test our hypothesis (see above), and the results obtained by implementing it, we need to define the participatory process. The two most commonly used definitions are participatory variety selection (PVS) and participatory plant breeding (PPB) (Witcombe *et al.*, 1996). There are important conceptual differences between the two. PVS is selection among (usually few) finished or nearly finished varieties, such as when farmers choose from on-farm variety trials, which are the very last stage of a breeding programme, and, very importantly, it is a linear process. By contrast, in PPB farmers participate in selection when genetic variability is at or near its maximum, such as selection between or within early segregating populations. PPB is also a cyclic process as we shall see later.

Other terms used to define various types of participation are participatory crop improvement (Witcombe *et al.*, 1996) and, more recently, client oriented plant breeding (Witcombe *et al.*, 2005).

PPB is a type of participatory research in which users are involved in the *design and implementation* rather than merely in the *testing* of a new technology as in non-participatory research. Therefore, while conventional plant breeding is largely a supply-driven process, PPB is largely a demand driven process (Ceccarelli and Grando, 2007).

A MODEL OF PARTICIPATORY PLANT BREEDING

The PPB programme we shall describe below is a collaboration between scientists and farmers, and from a biological point of view is based on three principles:

- Trials are grown in farmers' fields using individual farmer's agronomic practices ranging from low to high input.
- Selection is conducted jointly by breeders and farmers in farmers' fields, so that farmers participate in all key decisions.
- The traditional linear sequence scientist ➞ extension ➞ farmers is replaced by a team approach with scientists, extension staff, non-governmental organizations and farmers participating in all major steps of variety development.

Before introducing the model of PPB, largely derived from Ceccarelli and Grando (2005; 2007), we need to clarify that there are no fixed models in PPB. For the same crop, and even within the same country, different models may be required depending, among other factors, on the genetic structure of the final product and on how farmers handle on-farm genetic diversity prior to becoming involved in PPB. For example, in Eritrea barley is traditionally grown as a food crop in the form of genetically heterogeneous populations, but recently it has started to be grown also for malt production. In the first case, we use a population improvement method with nearly the entire breeding programme in farmers' fields to produce higher yielding heterogeneous food cultivars, while in the second we use a classical pedigree method with marker-assisted selection with part of the programme in the research station and laboratory to produce pure lines with better malting quality.

In the model we are using with a number of self-pollinated crops (barley, bread wheat, durum wheat, lentil and chickpea) and in a number of countries (Syria, Jordan, Egypt, Eritrea, Algeria and Iran) scientists make crosses, grow the F_1 and the F_2 on station, analyse the data, and keep a safely stored electronic copy of all the data. Farmers routinely evaluate and visually score the breeding material, adopt and name varieties, produce seed of the adopted varieties and commercialize their

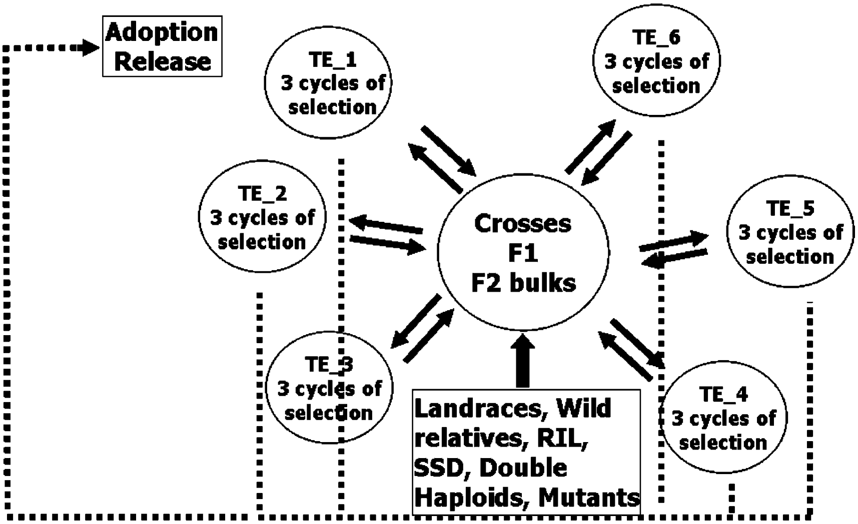

Figure 5. A model of participatory breeding programme used in self-pollinated crops in the hypothetical case of six target environments (TE).

seed. Occasionally they also set priorities, introduce methodological changes, select parents for crosses and choose the type of genetic material (e.g. improved vs landraces, populations vs hybrids).

The first breeding material we test in farmers' fields are bulk F_3 populations derived from targeted crosses; this is for the purely technical reason that the amount of seed in the F_2 is often insufficient for multi-location testing. Therefore if, for example, we make 150 crosses for a given target environment (a region, a country or a geographical area within a country), that target environment will receive, at the beginning of the programme, only the 150 F_3 bulk populations derived from those crosses.

On theoretical grounds, a given target environment includes villages which shows repeatable (over time) interactions with those in another target environment and non-repeatable interactions between them. Therefore, the villages are initially chosen based on differences in rainfall, soil type, farming system, type of genetic material, uses of the crop, farmers' typology (e.g. wealth, literacy, religion, gender, ethnic group, farm size), and they are subsequently re-defined based on the data which are progressively generated.

In the case of breeding programmes which do not have the resources for making crosses, the initial germplasm can be a collection of old varieties or a collection of landraces drawn from a gene bank and multiplied, or segregating populations received from other breeding programmes, such as those of the International Agricultural Research Centres. In a mature breeding programme, other types of materials (as shown in Figure 5) can flow into the participatory programme.

In each village, the bulks are tested for three years in farmers' fields in trials that we commonly call FIT (Farmer Initial Trials), FAT (Farmer Advanced Trials) and FET

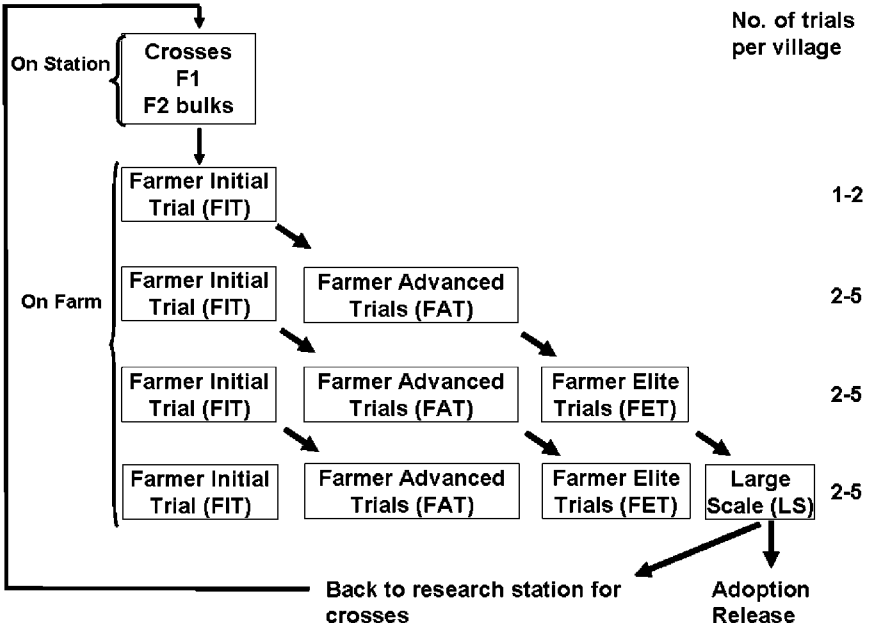

Figure 6. The sequence of the participatory breeding trials in one village: after the crosses are made on station where the F_1 and the F_2 are grown, the FIT (Farmer Initial Trials), FAT (Farmer Advanced Trials), FET (Farmer Elite Trials) and LS = (Large scale trials) are grown in farmers fields. When the model is fully implemented each village has one FIT, between four and eight FATs, FETs and LSs. The lines in the LS are candidates for adoption and are used on-station as parents in the crossing programme.

(Farmer Elite Trials). The initial yield trials are unreplicated trials with a number of entries, which varies depending on the crop and on the country. In Syria with barley, these include 165 entries and five controls common to all villages, while 30 plots are allocated to one or two systematic controls. In other countries, the number of entries in the FIT ranges from 60 to 100. When there is a large diversity in the crop, and when the farmers in different villages have different preferences, different villages receive, from the beginning of each breeding cycle, different breeding material, so that the total number of entries tested across all villages can be large (in the case of Syria it is more than 400 genetically different entries as we shall see later). In the villages receiving the same breeding material, the FIT are planted with a different randomization.

The FAT and FET are replicated trials with two replications. The three types of trials are all laid out as row and column designs, and the data are analysed with a spatial analysis using Genstat (Singh *et al.*, 2003). The analysis produces the best linear unbiased predictors of genotypic values (BLUPs), and a number of variables including heritability and its standard error.

The sequence of the trials is illustrated in Figure 6 in the case of one village. The FIT contains 200 plots each of 12 m^2; generally, there is only one FIT in each village. The number of plots and of entries varies according to the countries particularly in relation to the farm size of small farmers.

As a result of farmers' selection (described below), a number of entries (usually between 15 and 20) are promoted from the FIT to the FAT. Because selection in each village is independent from other villages and because the entries in the FIT are different, the number of entries in the FAT varies from village to village. The plot size in the FAT is three times larger than the FIT ($36\,m^2$). In each village there are a number of FATs, varying from two to five, depending on how many farmers are willing to manage this type of trial. In each village, the FATs contain the same entries since the selection from FIT to FAT is done by consensus. Each farmer decides the rotation, and the amount and the time of application of fertilizers and herbicides. Therefore, the FATs are planted within the same village under a range of conditions and management systems. During selection, farmers exchange information about the agronomic management of the trials, and rely greatly on this information before deciding which entries to select. Therefore, the breeding materials start to be characterized by their responses to environmental or agronomic factors at an early stage of the process.

Selection is repeated in the FAT, and the entries which are selected by consensus are tested in the FET, with a plot size twice as large as the FAT ($72\,m^2$).

To avoid the effect of different seed sources on the performance in the subsequent year, we grow on station a large seed multiplications plot of each of the entries tested in the FIT, FAT and FET. The trials are planted with a plot drill using a common seed source and the seed is treated against seed-borne diseases.

An essential component of the model is the process by which farmers perform their selection, and this takes place at three main levels:

- The farmers decide which type of germplasm they wish to receive, e.g. in the case of barley, two-row or six-row, black or white seed, improved or landraces, pure lines or populations. This decision is usually taken at the beginning of the programme and can be changed at any time.
- The farmers select visually in farmers' fields using a numerical score (generally from 0 = undesirable to 4 = best) while scientists measure a number of traits such as early growth vigour, plant height, spike length, grain yield, biological yield and kernel weight. Other traits measured occasionally are lodging resistance, reaction to diseases, cold damage and wilting due to drought stress. Phenology, as days to heading, is only measured in the multiplication plots on station because of its high heritability. Other traits, including physiological ones such as canopy temperature depression, carbon isotope discrimination and chlorophyll content can also be recorded.
- After data analysis (done by the scientists), the results are made available to the farmers in the form of tables written in their own language, and in a joint meeting with the breeders they decide which entries to promote to the following cycle.

Because the programme is structured in a cyclic fashion (the process is repeated every year), the quality of farmers' participation increases with time. It has recently expanded into areas such as setting priorities, introducing methodological changes, selection of parents, adoption of potential varieties, naming of varieties and seed production.

In some cases, farmers have gone as far as establishing small seed enterprises with advertising on local media.

After the three years of testing, farmers usually select from one to three entries to be planted in large scale (LS) demonstration plots; this is the first step in adoption (six years after the cross is made). In this case, both the seed from the on-station seed multiplication of the FET and seed produced on farm are used to plant the largest possible area.

When the programme is fully implemented, each village comprises one FIT, a number of FATs with entries selected from the FIT of the previous year, a number of FETs (equal to the number of FATs) derived from the FITs of two years earlier, and a number of LS demonstration plots derived from the FITs of three years earlier (Figure 6). This is what we meant earlier by PPB being a cyclic process. The entries promoted from FET to LS in the various villages are also included in the crossing block for a further cycle of recombination and selection.

Therefore, the programme follows a pragmatic approach based on the pyramiding of genes associated with adaptation and yield in a range of villages including those affected by drought. This is done by recurrent selection both within and across villages depending on the repeatability of G × L interactions.

In the case of Syria, the programme was initially implemented in nine villages (Ceccarelli *et al.*, 2000; 2003), extended to 11 in 2001 and eventually to 23 in 2004.

RESULTS AND DISCUSSION

The results obtained by implementing our model helped to clarify the role of PPB in relation to some of the main issues in plant breeding, namely, variety release, the role of molecular breeding, the precision of the trials, the effect on biodiversity, the efficiency of selection, gains with selection for drought tolerance and the type of germplasm.

Variety release

In most developing countries, the release of a new variety is an important process because, in principle, growing varieties which have not been officially released is illegal.

Generally the decision on variety release is based on the data generated by a special type of trial, usually called an on-farm trial (the name emphasizes that these are the only trials outside the research station) organized by the public organization responsible for agricultural research. In a number of countries, other organizations, public and private, can contribute lines to be tested in the on-farm trials.

The actual decision about release is taken by a special committee, called a variety release committee, usually chaired by the Minister of Agriculture, which after examining the evidence produced by the breeder, decides if the variety can be released for cultivation and with what name. In some cases the decision also indicates the area (either geographically or environmentally) where the variety is expected to perform well.

After the release, a small amount of breeder seed is made available to a public or private seed company, which then takes care of producing the large amount of seed

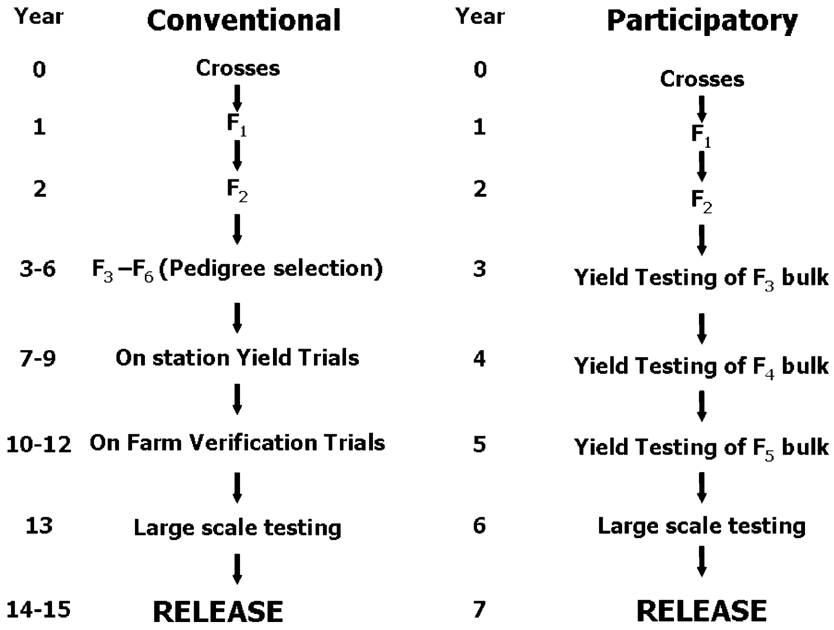

Figure 7. Time required to release a variety in a conventional breeding programme and in a participatory breeding programme in the case of a self-pollinated crop.

required to satisfy the demand of the farmers. However, in a conventional breeding programme and particularly in developing countries, the entire process is based on the *assumption* that farmers will buy the seed of the released variety, and therefore a large investment is made without knowing whether the variety will be actually grown, because at no point during the development of the variety, has the opinion of the farmers been sought. The result is that many of the varieties released are never grown by farmers.

In a conventional breeding programme, e.g. for a self-pollinated crop and following a classical pedigree method, it normally takes about 15 years to release a variety (Figure 7). With the method of PPB described above, the time is reduced by half. However, the comparison is biased because of the difference in the genetic structure of the material being released, i.e. pure lines in one case and populations in the second.

If populations are not acceptable to the variety release authorities, it is possible to introduce in the model a phase of pure line selection within the best bulks by selecting 50–100 heads in each of the selected bulks in the plots used for seed multiplication and grown on station. These are first grown as head-rows, then as two-row plots in the second year (if the corresponding bulk is promoted from FIT to FAT), and as six-row 7.5 m long plots in the third year (if the corresponding bulk is promoted from FAT to FET). Therefore, those bulks which reach the third year of yield testing have sufficient seed of the F3-derived F7 lines to be included as entries in the FIT. When the programme is fully implemented, the FIT, FAT and FET contain two types of breeding material, new bulks and pure lines derived from the best bulks of the previous cycle.

If, in a given country, the requirements for the genetic uniformity of the varieties to be released are very strict, only the pure lines will be considered as candidates for release.

In the case of pure line development, it can be shown that the time to variety release in a PPB programme is still 3–4 years shorter than the conventional programme based on the pedigree method, and again the comparison is biased because the conventional programme does not generate any information on farmers' preferences.

The method is therefore very flexible because: i) it allows selection between as well as within populations, and ii) it can generate populations, pure lines and eventually mixtures of pure lines. Similarly, when applied to cross-pollinated crops, PPB can be used to produce hybrids, populations and synthetics.

Molecular breeding and participatory plant breeding

In recent years several plant breeding programmes, particularly in developed countries, have incorporated molecular techniques extensively. Although these technologies are only a means to know the genotype of the breeding materials more rapidly and precisely, and therefore to make selection more efficient, molecular breeding is often seen as an alternative to conventional methods. This view ignores the fact that no matter by which methodology a new variety is produced, once it reaches the growers it will inevitably face the issue of adoption. Therefore, PPB can benefit in terms of efficiency and precision by the use of molecular techniques as much as conventional plant breeding.

One of the most obvious applications of molecular breeding to PPB is marker assisted selection (MAS), which is a method that uses molecular markers for indirect selection of traits that cannot be easily selected for using conventional methods, thus speeding up the process of conventional plant breeding and facilitating the improvement of these traits (Ribaut and Hoisington, 1998; Varshney *et al.*, 2006). In a participatory breeding programme, the identification of the traits to select for with the aid of a molecular marker takes place during the participatory phase and can actually be a contribution of farmers to the programme. This applies to traits both under the control of a QTL (quantitative trait locus, or genomic region associated with a phenotypic trait exhibiting continuous variation) (Varshney *et al.*, 2006) or of single genes. The actual implementation of MAS rests with the breeder or with the molecular breeder associated with the breeding programme. Other molecular techniques relevant to PPB include those which speed up the generation time, thus allowing testing of more than one generation in the same cropping season, and therefore a faster response to farmers' demands.

Farmers' participation may identify important traits about which little is known from classical or molecular genetics. This can help prioritize future mapping work, or may suggest new ways to use existing mapping populations which happen to segregate for the traits in question to acquire the information necessary to manipulate the traits to create those gene combinations which are desirable to farmers. Eventually, molecular techniques such as fingerprinting may be extremely useful for a molecular characterization and identification of varieties. The way in which the material produced by the use of molecular breeding techniques flows in to a PPB programme is shown in Figure 5.

Finally, the participatory breeding programme contributes to molecular breeding for drought resistance by making available for molecular studies lines identified as drought resistant by farmers' communities in a number of locations and years. The general objective of these studies is to understand the genetic basis of the drought resistance of these lines using molecular tools.

The first example is represented by Tadmor, a pure lines selection from the black-seeded landrace Arabi Aswad, adopted by a number of farmers in the driest areas of Syria. Tadmor is one of the parents of the mapping population Tadmor//ER/Apm developed at ICARDA and used extensively in studies which have revealed the chromosomal location of a number of traits related to drought tolerance. For example, Teulat *et al.* (2003), using this population, found that the long arm of chromosome 6H is involved in the control of relative water content, and a total of 10 QTLs for osmotic adjustment were identified (Teulat *et al.*, 1998; 2001). In the same population, two QTLs for carbon isotope discrimination were identified on chromosomes 2H and 4H (Teulat *et al.*, 2002). These were co-localized with QTLs for osmotic adjustment and 1000-kernel weight.

The mapping population Arta/*Hordeum spontaneum* 41-1 (one of the parents of the highly drought resistant lines described below and in Figure 8) has been used to localize QTLs for agronomic traits related to drought resistance, such as plant height under drought for which QTLs on chromosomes 2H, 3H and 7H were detected (Baum *et al.*, 2003; 2004). In this mapping population, QTLs were also identified for other traits associated with adaptation to the Mediterranean environment such as cold tolerance, days to heading and tiller number.

The picture which is emerging is that the superior performance of the breeding lines selected in water-limited environments does not have a simple basis but is associated with several traits, some of which possibly are associated with linkage blocks which have been shown to exist both in landraces and in *H. spontaneum*.

Precision of the trials

One issue which is frequently used to justify the need to conduct trials on research stations is the precision of the trials (Atlin *et al.*, 2001). Despite the example of the breeding programmes in Australia where yield trials have been planted in farmers fields for a long time, many national programmes are still reluctant to test the breeding material in the target environments outside research stations.

By comparing broad sense heritabilities (heritability is the ratio of the genetic variance over the total phenotypic variance) at different yield levels, we have found that trials in farmers fields and/or in low yielding sites are not necessarily less precise than trials in more favourable conditions (Al-Yassin *et al.*, 2005). Using the FITs conducted in Syria in 2004, 2005 and 2006, we have correlated the heritability and grain yields in the villages where the trials were conducted. There was a wide range of yields from near crop failure (14 kg ha^{-1}) up to 4179 kg ha^{-1} (Table 1) and we

Table 1. Average grain yield of barley (gy as mean of 165 entries in kg ha^{-1}) and heritability (h^2) in 25 villages in 2004–2006.

Village		2004		2005		2006	
Code	Name	gy	h^2	gy	h^2	gy	h^2
2	Mardabsi	1699	0.164	2396	0.502	2427	0.08
3	Shama	551	0.138	637	0.103	1604	0.00
4	Jern El Aswad	438	0.282	803	0.223	533	0.40
5	Baylounan	842	0.03	730	0.49	446	0.27
6B	El Bab†	14	0.328	972	0.435	817	0.57
6C	El Bab	380	0.6	discontinued	–	discontinued	–
7	Mailabieh	336	0.426	367	0	258	0.20
8D	Bari Sharki‡	1168	0.34	929	0.011	2484	0.26
8S	Bari Sharki	672	0.027	679	0	1526	0.29
9	Suran	3198	0.265	2991	0.341	4179	0.00
10	El Mghairat	367	0.194	751	0.208	–	–
11	Khanaser	665	0.288	966	0.379	1071	0.63
12	El Aalaimat	725	0.888	745	0.051	763	0.35
13	Makasem Khamseh	277	0.544	382	0.101	820	0.22
14	El Horieh	256	0.08	1442	0.5	498	0.17
15	Siebatt	388	0.355	838	0	879	0.00
16	Kherbet El Dieb	222	0.616	285	0.513	870	0.11
17	El Batraneh	2725	0.64	1831	0.212	1341	0.61
18	El Gherieh	809	0.451	385	0.688	1694	0.44
19	Khabab	2050	0.055	2786	0.633	367	0.65
21	Kherbet-Shlash	–	–	–	–	1315	0.04
22	Lahetha	1681	0.079	969	0.418	247	0.27
23	Emtan	1038	0.00	1420	0.012	262	0.34
25	Kafraya	796	0.258	2478	0.00	1062	0.29
26	Om El Amad	1190	0.132	1216	0.014	1509	0.00
27	Hardani	1664	0.00	1694	0.014	690	0.00

† In El Bab one FIT was planted in a barley–barley rotation (B) and the second in a cumin–barley rotation (C).
‡ In Bari Sharki one FIT was planted in deep soil (D) and the second in shallow soil (S).

found that the simple correlation coefficients were not significantly different from 0 ($r = -0.16$, in 2004; $r = 0.08$, in 2005; $r = -0.03$, in 2006).

In the future we plan to explore the possibility of improving the precision of the FIT by replacing the currently used unreplicated design in rows and columns with a partially replicated design.

Effect on biodiversity

An important suggestion is that by using PPB biodiversity will be better conserved and even enhanced as a joint effect of decentralized selection and the farmers' participation. This was tested using the data of the FIT-2001, FAT-2002, FET-2003 and LS-2004 breeding cycle in Syria (Table 2).

As indicated earlier, in each village the starting point of the breeding cycle in farmers' fields was the initial yield trials with 165 genetically different entries. The number of entries tested in the subsequent trials decreased to about 17 in the FAT, to

Table 2. Flow of germplasm, selection pressure, number of farmers participating in the selection and number of lines in initial adoption in one cycle of participatory plant breeding on barley in Syria.

	FIT	FAT	FET	LS
No. of different entries per village	165	17.3	7	3
Trials per village	1	3.2	3.4	2.8
Entries selected per village	17	8	3.5	1–2
No. of farmers selecting	9–10	8–9	8–9	8–9
Total no. of different entries	412	238	51	19

FIT: Farmer Initial Trials; FAT: Farmer Advanced Trials; FET: Farmer Elite Trials; LS: Large scale trials.

seven in the FET and to three in the LS. The number of trials per village varies from one in the case of the FIT, to about three in the case of the other trials. The number of lines selected by 8–10 farmers per village was on average 17, 8, 3.5, and between 1 and 2. Because different germplasm was tested in different villages, the total number of genetically different entries tested in the various trials was 412 in the FIT, 238 in the FAT, 51 in the FET and 19 in LS. In the case of Syria, the total number of different entries at *the end* of a breeding cycle in farmers' fields was higher than the number of lines the Syrian national programme tests at *the beginning* of the on-farm testing, which usually ends with one or two recommended varieties across the country.

Efficiency of selection

One of the assumptions of PPB is that farmers are able to conduct selection and there is already considerable evidence that this is indeed the case (Ceccarelli *et al.* 2000; 2003; Manu-Aduening *et al.*, 2006).

We have measured the ability of the farmers by comparing the top 20 entries for grain yield with the top 20 entries for the average farmers' score in the FITs conducted in 2004–2006 (Table 3). The percentage of entries in common, i.e. the frequency with which farmers were able to identify the highest yielding entries in a trial with 200 plots varies from zero to as much as 80 % with averages of 30 % in 2004 and 21 % in 2005 and 2006, and no significant differences between years and villages. In assessing these values it has to be considered that grain yield may not be the only selection criterion used during the visual selection. In fact, we have evidence that in the majority of the villages, particularly in those situated in the dry areas, the character most closely correlated with the average farmers' score is plant height.

Response to selection and drought resistance

Some examples of the gains obtained through PPB are shown in Table 4 for three contrasting villages with average rainfall in the three years ranging from 187 to 408 mm. The table shows only the lines which out-yielded consistently (i.e. in each of the three cropping seasons) the local landrace, which is still the most widely grown cultivar in the areas represented by these three villages. The average yield advantage (as the mean of the yield advantage in each year) was also calculated in relation to the improved control, a variety which has begun to be adopted in the three villages.

Table 3. Efficiency of farmers' selection expressed as % of the entries in the FIT 2004, 2005 and 2006 which are in common between the 20 highest yielding entries (12 % of the total number of entries) and the top 20 entries for the average farmers' score.

Village code	Village name	2004	2005	2006
2	Mardabsi	30.0	10.0	19.0
3	Shama	20.0	10.0	5.0
4	Jern El Aswad	50.0	25.0	0.0
5	Baylounan	15.0	30.0	20.0
6B	El Bab[†]	80.0	25.0	20.0
6C	El Bab	30.0	0.0	–
7	Mailabieh	15.0	15.0	40.0
8D	Bari Sharki[‡]	10.0	15.0	30.0
8S	Bari Sharki	35.0	50.0	25.0
9	Suran	15.0	25.0	10.0
10	El Mghairat	60.0	25.0	–
11	Khanaser	60.0	30.0	10.0
12	El Aalaimat	5.0	25.0	60.0
13	Makasem Khamseh	40.0	25.0	20.0
14	El Horieh	65.0	15.0	15.0
15	Siebatt	30.0	0.0	10.0
16	Kherbet El Dieb	45.0	30.0	30.0
17	El Batraneh	10.0	15.0	15.0
18	El Gherieh	20.0	25.0	10.0
19	Khabab	15.0	10.0	50.0
22	Lahetha	30.0	25.0	40.0
23	Emtan	30.0	20.0	25.0
25	Kafraya	25.0	15.0	00.0
26	Om El Amad	10.0	10.0	25.0
27	Hardani	15.0	25.0	30.0
Mean		30.4	21.1	21.2

[†] In El Bab one FIT was planted in a barley-barley rotation (B) and the second in a cumin – barley rotation (C).

[‡] In Bari Sharki one FIT was planted in deep soil (D) and the second in shallow soil (S).

The largest yield advantage (30 % over the local control and 27 % over the improved control) was found in the wettest of the three villages (Al Bab) where the FIT 2003 were planted in two fields, one after a barley crop (2003b) and one after a cumin crop (2003c). This was also the village with the largest variation between the three years with mean yields of all the entries ranging from 422 kg ha^{-1} in 2004 to 1355 kg ha^{-1} in 2003 in the trial planted after cumin. Despite this variation, the line SLB28-53/SLB21–81, derived from the cross between two pure lines extracted from the local landraces, out-yielded the local control by 30 % and by 47 % in the driest and the wettest of the three years, respectively.

In the other two villages, rainfall was considerably lower and yields, particularly in 2004 and 2005, were low. The average superiority of the best lines was 7 % and 9 % compared with the local control, and 2 % and 14 % compared with the improved control. The yield advantage was unrelated to the yield level.

These three villages were taken as examples of areas where no adoption of new varieties had taken place and farmers still grew the local landraces.

Table 4. Barley grain yield and yield advantage in FIT 2003, FAT 2004 and FET 2005 of entries identified by farmers in three villages with annual rainfall ranging from less than 200 mm to more than 400 mm out yielding consistently both the local and the improved checks.

	Rainfall (mm)				Grain yield (kg ha^{-1})				Yield advantage (%)[†]				
Village	2003	2004	2005	Entry	2003b[‡]	2003c	2004	2005	2003b	2003c	2004	2005	Mean
Al Bab	408.0	296.0	289.5	SLB28-53/SLB21-81	980	2900	487	1106	28.2	47.2	30.1	16.2	30.4
				Arta	773	1850	438	978	26.8	56.8	11.3	13.7	27.0
				A. Abiad	765	1970	375	952					
				Trial mean	*893*	*1355*	*422*	*1084*					
Bylounan	187.0	217.4	195.5	Arta/SLB22-74	1358		821	646	10.9		6.1	6.5	7.8
				Zanbaka	1354		840	592	0.3		0.7	9.0	3.3
				A. Aswad	1225		798	606					
				Trial mean	*1249*		*804*	*604*					
Melabya	275.9	176.0	182.7	Roho/4/Zanbaka/3/ER/Apm//Lignee131	1571		506	523	4.5		15.1	7.1	8.9
				Zanbaka	1677		418	409	93.7		21.0	28.0	14.3
				A. Aswad	1504		440	488					
				Trial mean	*1496*		*432*	*466*					

[†] For each village the first row gives the yield advantage over the local control (A. Abiad, A. Aswad) while the second gives the yield advantage over the improved control (Arta, Zanbaka).

[‡] In Al Bab there were two FITs, one planted in a barley–barley rotation (2003b) and one in a cumin–barley rotation (2003c).

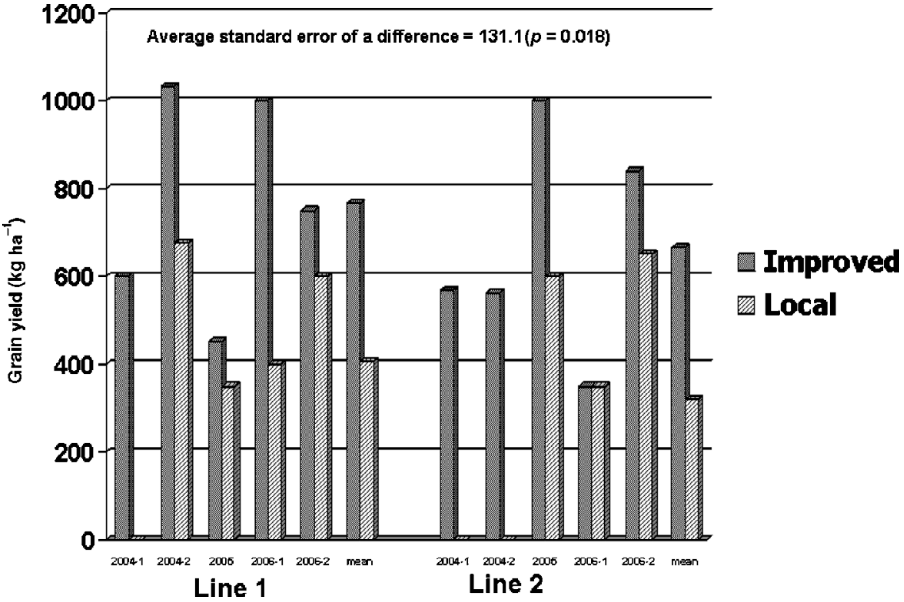

Figure 8. Grain yield under severe drought stress of two drought resistant lines in Syria in three years (2004, 2005 and 2006). The pedigrees of the two lines are: Line 1 (H.spont.41-1/Tadmor//SLB45–090/H.spont.41-2/3/H.spont.41-1/Tadmor//H.spont.41-1/Tadmor) and Line 2 (Arta/3/Arar/H.spont.19-15//Hml) and hence both of them are crosses with the wild relative of cultivated barley.

The programme has also produced the breeding material with the highest level of drought tolerance. This was identified in Syria in 2000, when the total rainfall in most areas was below average (ICARDA, 2001) and crop yields were severely affected. In some areas, the rainfall was so low that the seeds did not even germinate, and in many others the crop failed to produce any grain.

The FIT were affected by different intensities of drought: one extreme was Melabya (village 7 in Figures 1 and 2) with only about 50 mm rainfall in the entire season and no seed germination, and the other extreme was Suran (village 9 in Figures 1 and 2) with 252 mm rainfall and an average grain yield of 1.8 t ha^{-1} (ranging from 1.0 to 3.2 t ha^{-1}). The driest villages, where some new barley entries were able to produce some grain and/or some biomass were Bylounan (village 5) and Jurn Al-Aswad (village 4) with 87 and 121 mm, respectively, and Bari Sharky (village 8) with 130 mm. Average grain and biomass yields were very low, but some lines were able to produce between 300 and 500 kg ha^{-1} of grain and between 500 and 3000 kg ha^{-1} of biomass (Ceccarelli *et al.*, 2004).

These lines, all derived from crosses with *H. spontaneum*, have been multiplied and two of them were tested in farmers' fields in 2004, 2005 and 2006 on large plots of between 1 and 10 ha (Figure 8) in an area with 200 mm annual rainfall. The most remarkable result of these trials is that, in some cases, the improved lines produced about 600 kg ha^{-1} in situations where the farmers did not consider the local landrace worthy of being harvested (Line 1 and 2 in Farmer 1 in 2004 and Line 2 in Farmer

2 in 2004). On average these two lines out-yielded the local landrace by 89 % and 108 %, respectively ($p = 0.0128$).

Type of germplasm

A large amount of literature indicates that in many developing countries, and particularly for crops grown in drought-stress environments, landraces are still the backbone of agricultural production (Ceccarelli and Grando, 1999). Landraces are often able to produce some yield, even in difficult conditions where modern varieties are less reliable. For example, where farmers have adopted modern cultivars, they have kept the landraces in the most unfavourable areas of the farm (Cleveland *et al.* 2000).

The value of landraces as sources of drought tolerance is well documented in the case of barley in Syria (Ceccarelli and Grando, 1996) and in several others crops elsewhere (Brush, 1999). The comparison between barley landraces and modern cultivars under a range of conditions from severe stress (low inputs 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.
- The superiority of landraces is not associated 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 lines derived from landraces yield something whereas some 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.
- It is possible to find modern cultivars which under low-input and stress conditions yield almost as well as landraces, but their frequency is very low.

Recently (Ceccarelli *et al.*, 2000) compared fixed lines and segregating populations belonging to modern germplasm (100 entries) and to landraces (108 entries) in a range of locations which received between 193 and 460 mm rainfall with grain yields ranging from 280 to 4495 kg ha^{-1} (Table 5). In the four locations with average grain yields higher than 2500 kg ha^{-1}, both the breeder and the farmer selected slightly more modern germplasm (nearly 61 %) than landraces. By contrast, in the five locations with grain yields ranging from 280 to 1415 kg ha^{-1}, the majority of the selections (more than 70 %) were landraces, and this was particularly evident in the choices made by the farmers. In the highest yielding locations the modern germplasm out-yielded the landraces by 22 %, while in the lowest yielding locations the landraces out-yielded the modern germplasm by 24 %.

Another aspect of the relationship between the type of germplasm and drought resistance is the buffering capacity of heterogeneity. This might explain why it has been difficult traditionally to out-yield landraces consistently with genetically uniform modern germplasm in areas where rainfed crops are commonly grown under water-limited conditions. Recently Einfeldt *et al.* (2005), using pure stands of double haploid

Table 5. Rainfall, average grain yield (mean ± *s.e.*), of 208 barley entries in the nine villages where the participatory breeding programme was initially implemented and Breda and Tel Hadya (two research stations) and number of modern and landraces entries selected by farmers and breeders (modified from Ceccarelli *et al.*, 2000).

Location	Rainfall (mm)	Grain yield (kg ha^{-1})	Selected by farmer (F) or breeder (B)	Total	Modern	Landrace
Ibbin	436	3248 ± 81	F	11	11	0
			B	73	53	19
Ebla	460	2857 ± 58	F	11	9	2
			B	64	40	22
Tel Brak	278	3685 ± 69	F	13	3	9
			B	74	34	37
Jern El Aswad	284	1415 ± 51	F	9	0	8
			B	71	28	40
Baylounan	193	280 ± 13	F	6	0	6
			B	82	29	49
El Bab	350	376 ± 15	F	11	0	10
			B	71	22	45
Mailabieh	241	713 ± 29	F	10	3	7
			B	66	24	39
Bari Sharki	248	1017 ± 36	F	14	3	10
			B	91	37	50
Suran	303	2515 ± 46	F	10	5	5
			B	105	51	50

Table 6. Relative (%) effects in barley of heterozygosity in five environments (TH: Tel Hadya; BR: Breda; F: + fertilizer) for traits with significant heterozygosity × environment interactions; figures in brackets refer to total precipitation during September to August (modified from Einfeldt *et al.*, 2005).

Trait	TH96 (405 mm)	BRF96 (360 mm)	BR96 (360 mm)	TH95 (313 mm)	BR95 (244 mm)
Grain yield	−1.2	5.8**	16.7**	17.3**	45.6**
Harvest index	−6.1^{+}	1.3	2.0	9.6**	23.6**
Thousand grain weight	0.3	1.5	3.6**	7.7**	7.6**
Plant height	2.9*	10.7**	6.5**	7.1**	5.3**

$^{+}$, *, **significantly different from zero at the 0.1, 0.05, 0.01 probability levels, respectively.

(DH) lines, mixtures of DH lines (heterogeneous populations) and F_2 populations derived from crosses between the DH lines (a combination of heterogeneity and heterozygosity) found that while the heterogeneity had an advantage only on grain yield, the effect of heterozygosity was larger and was evident in all traits. More importantly, the heterozygosity × environment interaction was significant for grain yield, harvest index, 1000-grain weight, and plant height (Table 6). In the case of grain yield, the relative effect of heterozygosity increased substantially with increasing levels of stress. For the harvest index, a significant negative effect of heterozygosity was observed in Tel Hadya 1996. Under terminal drought stress only there was no significant effect of heterozygosity, while the superiority of the F_2 populations over the DH lines mixtures increased substantially in the environments with both pre-flowering and terminal drought. The advantage of the F_2 populations for 1000-grain weight increased with increasing stress levels, and was significant in the three lowest yielding environments only.

CONCLUSIONS

The main conclusions of this paper are that i) agricultural areas where crop production is limited by water availability represent a heterogeneous population of target environments, and ii) yield increases are possible even with conventional breeding by exploiting repeatable genotype × locations interactions in a decentralized breeding programme. Superimposing farmers' participation increases the efficiency and the effectiveness of the delivery phase of the breeding programmes, making sure that the final products are adapted not only to the physical (climate and soil) but also to the socio-economic environment and to the needs of the clients. This confirms that PPB can be targeted (focused on the right farmers), relevant (responding to real needs, concerns and preferences) and appropriate (able to produce results that can be adopted) (Bellon, 2006).

Increases in crop production are likely to come from the combined result of both agronomy and breeding (Anderson *et al.*, 2006; Parry *et al.*, 2005; Peterson and Westfall, 2004). However, farmers in the dry areas of developing countries, faced with the necessity of managing the high risk associated with rainfed farming in such areas, often do not have the technical and the financial means needed for better management. The financial resources needed may be generated by higher yielding varieties, specifically adapted to the unpredictable conditions of dry areas. The paper has also shown the beneficial effect of PPB on biodiversity which is now recognized to have a major potential role in maintaining yields under adverse shocks (Di Falco and Chavas, 2006) and therefore in reducing farmers' exposure to risk.

It is unanimously recognized that breeding for water-limited environments is difficult and, in fact, has improved yield at about half the rate achieved for crops grown in higher rainfall regions (Turner, 2004). It is also recognized that this is due to the complexity of drought tolerance, which has been found to be associated with several morpho-physiological traits. The use of these traits as selection criteria for drought tolerance has had limited success because the strength of the relationship between each individual trait and drought tolerance changes depending on the particular type of water-limited environment (Ceccarelli *et al.*, 1991). It is because of this complexity that attempts to improve yield under drought by marker assisted selection has yet to contribute significantly to crop improvement (Parry *et al.*, 2005).

Even, when the combined use of quantitative genetics and genomics together with appropriate agronomic practices make selection for yield under drought more efficient, we shall still need to make sure that the varieties are accepted and grown by farmers.

The methodology presented in this paper, while still relying heavily on phenotypic (empirical) recurrent selection, has been designed to make full use of biotechnological tools, and addresses specifically the last and usually the most difficult step in a plant breeding programme, which is the acceptability of the final product by the users. This is particularly relevant in developing countries where it is important to ensure the maximum return of the scarce resources available to plant breeding.

Acknowledgements. The authors acknowledge several hundreds farmers and many scientists, extension workers, seed specialists and non-governmental organizations for their contribution to the development and refinement of this programme. We also thank the OPEC Fund for International Development, the Government of Italy, the Government of Denmark, Der Bundesminister für Wirtschaftliche Zusammenarbeit (BMZ, Germany), the International Development Research Centre (IDRC, Canada), the System Wide Program on Participatory Research and Gender Analysis (SWP PRGA), and the Water and Food Challenge Program of the CGIAR for their financial support.

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