

Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity

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Abstract

Genotype by Environment (GxE) interactions are commonly seen as one of the major complications in plant breeding and have been widely discussed, particularly in relation to the choice of the selection environment(s).

Here GxE interactions are discussed in relation to plant breeding programs aimed at improving crop production in difficult environments where crop yields are low and crop failures are frequent, mostly due to unfavorable climatic conditions. These environments are highly variable for the specific combinations of abiotic and biotic stresses in any particular cropping season. However, the frequency of low yielding seasons is very high. Because of the high risk of crop failures, inputs such as fertilizers, weed control and pesticides are not used, and often irrigation is not available.

Subsistence farmers in these environments have not benefited from the spectacular yield increases obtained by plant breeding in environments which are naturally favorable or could be profitably made favorable by using inputs.

Experimental evidence from a number of crops in different geographical areas suggests that when different cultivars or breeding lines are tested in a sufficiently large environmental range, GxE interactions of the crossover type are of common occurrence. However, many breeders still believe that selection should be conducted under optimum conditions for plant growth because these conditions maximize heritability. Consequently, most selection work in developing countries, particularly in the early stages, is done in favorable conditions or in high-input experiment stations. If there are GxE interactions of crossover type, and the selection and the target environments lie at opposite sides of the crossover point, breeding materials developed in favorable conditions or in high-input experiment stations are not likely to perform well in difficult environments.

A strategy to maximize yield when GxE interactions are large and repeatable requires the exploitation of specific adaptation through separate plant breeding programs using different methodologies and type of germplasm.

International breeding programs can exploit specific adaptation by devolving selection work to national scientists. An example of how this can be achieved is given using the case of the ICARDA barley breeding program in north Africa.

Farmers' participation in selection under their own environmental and agronomic conditions is eventually envisaged as a way to maximize specific adaptation, and to speed up the transfer of new cultivars and their adoption. One important consequence of breeding for specific adaptation is that the number of cultivars of a given crop grown at any moment in time will be large and this will maintain more genetic diversity within a crop than with breeding for broad adaptation.

The use of a positive interpretation of GxE interactions implies adapting cultivars to their environment, rather than modifying the environment to fit new cultivars. Therefore, breeding for specific adaptation is a more sustainable strategy than breeding cultivars that can only express their superiority at high levels of inputs.

Introduction

Genotype by environment (GxE) interactions are almost unanimously considered to be among the major factors limiting response to selection and, in general, the efficiency of breeding programs. GxE interactions become important when the rank of breeding lines changes in different environments. This change in rank has been defined as crossover GxE interaction (Baker, 1988).

GxE interactions in general, and GxE interactions of crossover type in particular, are considered to have a negative impact on the success of breeding programs, because breeders search for a few widely adapted cultivars. Whilst this is probably the best strategy in the case of breeding programs in developed countries targeted to favorable environments, it has been suggested (Ceccarelli, 1989; Hildebrand, 1990; Stroup *et al.*, 1993) that, in case of unfavorable environments, breeders may look at GxE interactions in a different way.

Throughout this chapter unfavorable environments are defined as those where crop yields are commonly low due to the concomitant effects of several abiotic and biotic stresses. The semiarid areas of Syria, where barley is the predominant crop, are a good example of such environments where not only low annual rainfall, but also rainfall distribution, low winter temperatures, high

temperatures and hot winds from anthesis to grain filling are important abiotic stresses. Although the frequency, timing, intensity and duration of each of these stresses, as well as their specific combinations, vary from year to year pre-anthesis water stress is common and post-anthesis water stress is the rule. Figure 1 shows the cumulative frequency distribution of grain yields of barley in the on-farm testing program between 1982 and 1994 in two climatic zones of Syria (zone C receiving less than 250 mm annual rainfall, and zone B receiving less than 250-350 mm annual rainfall). In zone C low yields of barley are common, crop failures occur one year out of ten, and yields above 2.5 t ha^{-1} are expected less than 20% of the time. By contrast, in the relatively favorable environments of zone B yields of 1 t ha^{-1} or less have a frequency of about 10%, and yields above 2.5 t ha^{-1} occur more than 40% of the time.

Because of the high probability of low yields and crop failures in unfavorable environments, the use of inputs such as fertilizers, pesticides and weed control is seen by farmers as risky. Therefore, the adoption of "improved agronomic practices" has been very limited, and the only economic solution to increase crop yields in unfavorable environments is through breeding. However, empirical breeding for these environments has been historically much less successful than for favorable environments, or for environments which could be made favorable by the use of fertilizer, by chemical control of weeds, pest and diseases, and by irrigation.

The integration of physiological traits in breeding programs for unfavorable environments is one avenue to increase the efficiency of breeding which has been discussed extensively in the literature (Richards, 1991; Blum, 1993; Bidinger *et al.*, 1995 **this book**). While the need of a better understanding of the role of physiological traits and of environment characterization is covered elsewhere in the book, the main objective of this chapter is to address the general question of why empirical breeding has not been very effective in improving crop production in unfavorable environments. In particular, the chapter will discuss one possible strategy to avoid and exploit GxE interactions in breeding programs for unfavorable environments with emphasis on issues such as the choice of the selection environment, specific versus wide adaptation, genetic uniformity versus genetic diversity.

Genotype by environment interactions of crossover type

Since GxE interactions of crossover type pose major problems in breeding programs, the question of how frequently these interactions occur is important. In general, when different lines or cultivars of a given crop are evaluated in a sufficiently wide range of environments, GxE interactions of crossover type seem to be very common.

Examples of GxE interactions of crossover type can be found in the literature in a range of crops and environments, and for various stresses: Breese (1969) in cocksfoot, Arboleda-Rivera and Compton (1974), Hildebrand (1984) and Loffler *et al.* (1986) in maize, Simmonds (1984a) in sugarcane, Lawn (1988) in chickpea, Ceccarelli (1989), Ceccarelli and Grando (1991) and Jackson *et al.* (1993) in barley, Blum and Pnuel (1990) in wheat, Virk and Mangat (1991) in pearl millet, and Shannon and Francois (1978) in muskmelon in relation to salt tolerance.

In barley we routinely test breeding material in sites differing in total rainfall, soil fertility and winter temperatures, with an average four-fold difference in mean yields between the two most contrasting sites (Table 1). When we compared, at each of the two most contrasting sites, the highest yielding lines at each site, a consistent pattern was observed over the last ten years (Table 2). When compared in high yielding sites (HYE), those lines which had the highest yield in the lowest yielding site (GL) yielded significantly less than the lines which had the highest yield in high yielding sites (GH). When the comparison was made in low yielding sites (LYE), those lines which had the highest yield in high yielding sites (GH) yielded significantly less than the lines which had the highest yield in low yielding sites (GL).

A similar picture emerges from the few published data on genetic correlation between yield measured in high and low yielding conditions (Atlin & Frey, 1989, 1990; Ud-Din *et al.* 1992; Ceccarelli *et al.* 1992; Cooper and DeLacy, 1994). This indicates that, as a general phenomenon, high yielding lines under optimum growing conditions do not perform well under poor growing conditions, and vice-versa. This is hardly surprising as physiologists have long recognized, with specific reference to drought, that different physiological mechanisms and different phenologies are associated with high yield in favorable conditions and high yield in unfavorable conditions (Hsiao, 1982; Blum, 1993).

Figure 2 shows an example of GxE interactions of crossover type in barley. Lines selected for high grain yield either in high yielding sites (YP) or in low yielding sites (YD) between 1988 and 1990 were compared in 21 location-year combinations between 1991 and 1994. The 21 location-year combinations were ranked for the average grain yield of all the 64 barley lines in the trial and grouped in five groups (from very low yielding to very high yielding). Each group was made of four location-

year combinations except the intermediate group which was made of five. The YP lines yielded more than the YD lines in the medium to high yielding location-year combinations and the YD lines yielded more than the YP lines in the low and very low yielding location-year combinations. Between the medium and low-yielding location-year combinations the YP and YD lines crossover.

Before discussing the implications of GxE interactions of crossover type, it is necessary to specify that the range of environments in Fig. 2, and their associated yield levels, may represent either variation over time within one given geographical area, or variation over space (between different geographical areas within or across countries). The discussion which follows assumes that the yield levels below the crossover point are fairly representative of variation over time within a given geographical area. In areas of this type, the probability of climatic events that will determine yields above the crossover point are possible but rare as shown in Fig. 1.

With this assumption in mind, there are four points to make about multi-environment trials such as those illustrated in Table 2 and in Fig. 2.

Firstly, is that the definition of unfavorable environments plays a key role in determining breeding strategies. If we define unfavorable environments as those with an average yield around (in this case) 2.3 t ha^{-1} , then the YP lines are well adapted to both unfavorable and favorable environments (broadly adapted). However, if we define unfavorable environments as having an average yield below 2.3 t ha^{-1} , the broad adaptation of the YP lines has a lower limit at the crossover point. Defining as unfavorable environment an environment with an average yield at or above the crossover point is often justified for some crops. Taking again Syria as an example, bread wheat is cultivated only in areas with more than 300 mm annual rainfall, it overlaps with barley at the wettest end of the production zone of the latter, and in dry years it receives one or more supplemental irrigation. Therefore, the probability of yields lower than 2 t ha^{-1} is considerably less for wheat than for barley, and this may result in the absence of crossover and hence in different breeding strategies for the two crops. The effect of the definition of unfavorable environments on breeding strategies is well evident in Calhoun *et al.* (1994).

The second point relates to the type of comparisons made in multi-environment trials. The performance of lines such as the YP lines in Fig. 2 (selected in optimum environments) is often compared either with the average of all the lines in the trial (it is unclear what this comparison means), or against a local check. Their superiority over the mean of the lines or over the check is then taken as an indication of broad adaptation. Very seldom the comparison is made with lines selected in stress environments below the crossover point (such as the YD lines). When this is done, as in Table 2 and Fig. 2, the YP lines are still broadly adapted, but to a narrower range of environments.

The third point is that the presence of a crossover GxE interaction has often been neglected by either testing breeding material developed for favorable environments in foreign countries or by conducting selection and testing only above the crossover point, and particularly in high input experiment stations. Fig. 2 shows that conditions in which selection is conducted in experiment stations could be well above the hypothetical crossover point in relation to the conditions in farmers' fields. When lines are evaluated in many locations and selection is made for high average yield across locations, this is equivalent to selection for responsiveness to favorable conditions (Simmonds, 1991). Even shuttle breeding between two contrasting environments can miss the presence of crossover GxE interactions if both environments are above the crossover point. As the yields of many poor farmers are below the crossover point, the chances of their being supplied with improved, stable germplasm is low.

The fourth point is that the existence of a crossover GxE interaction has been allegedly disproved by the release of cultivars for low yielding environments (Byerlee, 1994). This argument neglects the fact that many of these cultivars have never been adopted by farmers or have been adopted in a different environment (Maurya *et al.*, 1988; Jansen *et al.*, 1990; Byerlee and Husain, 1993).

Hildebrand (1990) and Stroup *et al.* (1993) argued that, in the presence of GxE interactions of crossover type, breeders have traditionally selected lines which were, on the average, the highest yielding, discarding the top yielding lines at either extremes. They defined this breeders' attitude as "negative interpretation of GxE interactions". Such a negative interpretation of GxE interactions is caused by the search for widely adapted lines to accommodate large scale centralized seed production (Davis, 1990).

By contrast, a positive interpretation of GxE interactions (Ceccarelli, 1989; Hildebrand, 1990; Stroup *et al.*, 1993; Ceccarelli, 1994) recognizes the importance of specific adaptation and leads to the selection of lines specifically adapted to favorable environments (such as the YP lines in Fig. 2), and of lines specifically adapted to unfavorable environments (such as the YD lines in Fig. 2).

The concepts of positive interpretation of GxE interactions (see also Simmonds, 1984b, p. 359-360) is similar to the strategy proposed by Cooper and De Lacy (1994) and by Cooper *et al.* (1995 **this book**) in presence of GxE interactions which are large and repeatable. While issues such as how to deal with GxE interactions which are not repeatable, and which analytical tools are more appropriate to understand the nature of GxE interactions are covered elsewhere in the book, the rest of this chapter will deal with issues in breeding for specific adaptation from both a national and an international perspective.

Selection for specific adaptation

The main conclusion of the previous section is that, in presence of repeatable GxE interactions, the best breeding material for unfavourable environments can not be identified by conducting selection for yield in favorable environments or under the favorable conditions of experiment stations. Therefore, selection for specific adaptation implies the need for direct selection in unfavorable environments.

However, and particularly in developing countries, most plant breeders only select in optimum environments (Simmonds, 1991). The most common justification for this is the lower heritability associated with low yielding, unfavorable environments (van Oosterom *et al.*, 1993).

The theory of correlated responses to selection (Falconer, 1981, 1990) shows that not only heritability, but also the genetic correlation coefficient has to be considered before deciding which is the optimum environment for selection. However, even if we want to consider heritability alone, the experimental evidence that heritability in low yielding conditions is lower than in high yielding conditions is far from unanimous (Table 3).

Of particular interest are the data of Pederson and Rathjen (1981) (Table 4), which suggest a high degree of independence between yield levels and magnitude of heritability ($r = -.034$). In two sorghum populations, Zavala-Garcia *et al.* (1992) found that mean yield and heritability were positively correlated ($r = 0.69^{**}$) in one population, but independent ($r = -0.05$) in the second (Fig. 3). Our experience with barley (Singh and Ceccarelli, 1995) and recent data on wheat (Cooper and DeLacy, 1994) also suggests no relationship between yield level and magnitude of heritability. Therefore, the conclusion that heritability in low yielding environments is lower than in high yielding environments is not supported by experimental evidence (see also Simmonds, 1991).

The magnitude of heritability is affected by the type of genetic material. We suspect that the genetic material used in those studies where heritability in low yielding environments was lower than in high yielding environments was selected in high yielding environments and then tested in low yielding environments. If GxE interactions of crossover type exist, this implies a low average adaptation of this material to low yielding conditions, reduced genetic variation, hence low heritability.

Selection in unfavorable environments

Breeding for unfavorable environments based on selection (not merely testing) in the target environments is undoubtedly more difficult than selection for favorable environments largely because of the year-to-year variation. Procedures and methodologies developed for favorable environments need to be modified. Our methodology is based on the following principles:

- a. Breeding material (including parental material and segregating populations) is evaluated in the target environments using farmers' agronomic practices, including rotations. In the driest site (long term average rainfall of 233 mm) this means no use of fertilizers, pesticides and weed control. Farmers' fields are inspected one or two cropping seasons earlier and those where the farmer's crop is sufficiently uniform are selected as experiment sites. Concurrently, the material is evaluated at the main experiment station (long term average rainfall of 373 mm) with a level of inputs commonly used in moderately favorable areas. In all the experiment sites the material is evaluated strictly under rainfed conditions.
- b. Experimental designs have evolved from the randomized block design to the lattice design -lattice design (introduced in 1993). This has progressively reduced C.V.'s.
- c. Segregating populations are evaluated as bulks for three years taking advantage of the large year-to-year variation in total rainfall, rainfall distribution and temperature patterns. Each year bulks yielding less than the check are discarded. Individual plant selection is done only within the selected bulks.
- d. Selection is done for high grain yield at each of the experiment sites, regardless of the performance in other experiment sites. This promotes breeding material with specific adaptation without penalizing breeding material with environmental broad adaptation.

In the case of the barley breeding at ICARDA, direct selection in unfavorable environments revealed that locally adapted landraces could be a useful source of breeding material. This is shown by the comparison between lines from Syrian landraces and lines unrelated to Syrian landraces (Table 5). The comparison was made using different sets of breeding lines each tested in 8-10 location-year combinations. We compared the two types of breeding material for yield under stress (defined as the average grain yield in location-year combinations with average yield lower than the means of all testing sites minus one standard deviation) and for yield in non-stress conditions (defined as the average grain yield in location-year combinations with average yield higher than the means of all testing sites plus one standard deviation). The yield under stress of landraces was between 25 and 61% higher than non-landraces, while their yield in non-stress conditions was between 6 and 18% less than non-landraces. The range for YS shows that under stress conditions the lowest grain yield of landraces was always higher than the lowest grain yield of non-landraces. Therefore, the risk of crop failures is lower with landraces than with non-landraces. This characteristic of landraces, perceived by farmers as stability, and their yield advantage in stress conditions would have been missed had the evaluation taken place only in high yielding environments. Repeated cycles of selection only in high input environments reduce the frequency of lines specifically adapted to stress environments, and viceversa. This is shown by the yield in unfavorable conditions of barley lines selected in favorable conditions (indicated as YP) or in unfavorable conditions (indicated as YD) (Table 6). The selection took place in three periods of yield testing of three years each (1986-88, 1987-1989 and 1988-1990) as described under d) earlier. The selected lines were tested in a range of 21 location-year combinations between 1991 and 1994. The Table shows the average yield in the five location-year combinations with the lowest yields (ranging from .354 to 1.155 t ha⁻¹) as an estimate of yield in unfavorable conditions. In the five location-year combinations the average yield of the YD lines was between 25% and 46% higher than the YP lines, the top YD line was between 6% and 19% higher yielding than the top YP line, and none of the YP lines outyielded the best check which, not surprisingly, was the locally grown landrace. It was also not surprising that the larger genetic gains over the best check were made with the group YD3 which was entirely made of pure lines selected from the local landrace.

These data indicate that a) it is indeed possible to make progress with selection under unfavorable conditions, and b) that a large amount of potential improvement in unfavorable environments is missed by breeding programs using only selection in favorable conditions.

The combined use of direct selection in unfavorable conditions and of adapted germplasm has recently led to the adoption by Syrian farmers of three cultivars, one for zone B and two for zone C (described in Fig. 1).

Specific adaptation and international breeding programs

International breeding programs aim to assist national programs to increase agricultural production by developing superior cultivars. This is traditionally done through very large breeding programs which develop fixed or semi-fixed lines with an average good performance across many environments (often high input experiment stations). The interaction between international and national programs has been largely a one-way, "top-down" process (Simmonds and Talbot, 1992) where international programs develop germplasm and national programs test and eventually release it as cultivars. This has often excluded the use of locally adapted germplasm, which often performs poorly in favorable conditions such as those of experiment stations, and encouraged its displacement.

The adoption of a positive interpretation of GxE interactions by international breeding programs has been advocated as a way to address the need of small, resource-poor, subsistence farmers, who have been by-passed by the Green Revolution (Stroup *et al.*, 1993).

To exploit specific adaptation fully and make positive use of GxE interactions, an international breeding program could devolve most of the selection work to national programs by gradually replacing the traditional international nurseries with earlier generation material. Early distribution of breeding material reduces the danger of useful lines being discarded because of their relatively poor performance at some test sites. This problem is illustrated by 288 barley lines evaluated both in the Maghreb countries (Libya, Tunisia, Algeria, Morocco) and in ICARDA's preliminary yield trials grown at three sites in Syria (ranging from moderately favorable to unfavorable) in 1991/92 (Table 7). In the Maghreb countries visual selection was used, whereas in Syria selection was for yield potential, yield under stress, and heading date. 103 entries were selected in Syria and 154 in the Maghreb but only 49 of these were selected both in Syria and in Maghreb. More than half (52.4%) of the 103 lines selected in Syria were discarded in Maghreb, and almost 70% of the 154 lines selected in Maghreb were discarded in Syria. This gives a measure of the danger of discarding lines potentially useful in other areas in a centralized breeding program.

ICARDA's barley breeding program has started recently a gradual process of devolution of selection work to the four Maghreb countries (Ceccarelli *et al.*, 1994). When fully implemented, national programs in north Africa will receive from ICARDA's barley breeding program only targeted F₂ segregating populations (based on crosses partly designed by national programs), and yield trials consisting of lines derived from these F₂'s selected in-country. Selection between F₂ populations will be in the different agroecological environments within each country under conditions as similar to farmers' fields as possible. Lines selected from superior F₂ populations will be advanced at ICARDA and then yield tested in different locations within each country.

Barley and lentil breeding for the Anatolian plateau in Turkey, lentil breeding for the Indian subcontinent, and durum wheat breeding for Morocco are based on the same philosophy.

Specific adaptation, sustainability and biodiversity

Breeding for sustainability has been defined as a process of fitting cultivars to an environment instead of altering the environment (by adding fertilizer, water, pesticides, etc.) to fit cultivars (Coffman and Smith, 1991). Also, it has been recognized that the key to increased production with fewer external inputs, a condition which is more self-sustaining, less harmful to the environment, and yet productive enough to meet the increasing demand for food, will be through a reevaluation of the identification and use of selection and testing environments (Bramel-Cox, *et al.* 1991).

This chapter shows that for a typical crop of marginal and unpredictable environments such as barley, it is possible to exploit genetic differences for specific adaptation to marginal environments under farmers' conditions and improve yield without additional inputs. Breeding for specific adaptation not only offers a solution on how to improve agricultural production in marginal environments, but can do so in a sustainable way. This breeding philosophy, based on a positive interpretation of GxE interactions, is in contrast with the common belief that the introduction of inputs, such as fertilizer and irrigation, to raise the yield potential is an essential prerequisite for successful breeding work. Breeding for an agronomically improved environment dictates the type of germplasm which will best exploit it, and is based on genetic uniformity-the reverse of the biological diversity requisite for minimizing risk in most natural systems (Wilkes, 1989).

The use of high input selection environments is largely responsible for the trend of modern plant breeding towards narrowing the genetic base of our crops accompanied by a trend towards homogeneity: one clone, one pure line, one hybrid (Simmonds, 1983). Although genetic uniformity has been questioned in developed countries (Wolfe, 1991), it is still very popular in breeding programs and seed production systems of developing countries at both the national and international level. This is in contrast with the genetic diversity that characterizes agriculture in marginal environments: the genetic diversity is either in the form of mixed cropping or in the form of genetically heterogeneous cultivars, or both. Genetically heterogeneous landraces (also called farmers' varieties, old cultivars or "primitive cultivars") are still the backbone of agricultural systems in many developing countries, mainly in marginal environments where their replacement by modern, genetically uniform cultivars bred for favorable environments has proved to be a difficult task at the levels of inputs farmers can afford.

Breeding for specific adaptation to unfavorable environments implies a reevaluation of the role of genetic resources such as landraces which can play an important role because they possess adaptive features to these environments. This is the first consequence on biodiversity of breeding for specific adaptation.

A second consequence of exploiting specific adaptation on biodiversity is that the number of cultivars (not necessarily homogeneous) of a given crop grown at any time will be large. The benefits of maintaining genetic diversity within a crop over large areas has been discussed extensively in the literature in relation to resistance to pests and diseases and does not need further justification. The major disadvantage with breeding for specific adaptation is how to distribute many cultivars among farmers given the difficulties for conventional seed production systems. However, the distribution of specifically adapted cultivars to resource-poor farmers does not have to follow the conventional release-seed production-seed certification schemes used in developed countries. Indeed, there are examples of successful distribution and adoption of cultivars through non-market methods (Grisley, 1993).

The problem of transfer and adoption of new cultivars can be possibly solved by what can be considered the most extreme use of a positive attitude towards GxE interactions, i.e. farmers' participation in selection under their own conditions.

Maximizing specific adaptation through farmers' participation

The idea of farmers participating in the development of new technology is not new. It has been

introduced in 1982 (Rhoades and Booth, 1982) as "the farmer-back-to-farmer model", later modified into the "farmer-first-and-last-model" (Chambers and Ghildyal, 1985), and more recently has been discussed by Sperling *et al.* (1993) and Stroup *et al.* (1993). Using Sperling's terminology, a "formal breeding programs" can be shortly described as a sequential and cycling process (Fig. 4a) in which 1) an extremely large amount of genetic variability is continuously created, 2) this variability is drastically reduced through selection (we have seen that this is often done in conditions which have little in common with those of subsistence farmers), and 3) the few lines surviving step 2 are presented to farmers who are asked to verify if the choices made for them are appropriate.

The process has been very effective for those farming systems which are sufficiently similar or not too dissimilar from those on experiment stations. Therefore, it has been used as a model also when the target environment was very different from that of experiment stations, and it is common knowledge that the process has been ineffective for unfavorable environments. The reason is likely to be associated with GxE interactions. It is also possible that plant characteristics which are used as selection criteria in a high yielding environment, are not those which give the future cultivar an advantage when grown by a subsistence farmer. Indeed, there is evidence that 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 *et al.*, 1993). Typical examples are crops used as animal feed, such as barley, where breeders often use as the sole selection criterion grain yield which usually brings with it high harvest index and lodging resistance. However, in unfavorable environments lodging is not often a problem because of moisture stress, and farmers are interested not only in grain yield, but also in forage yield and in the palatability of both grain and straw.

There is also evidence that, when breeders and farmers select in similar environment, farmers' selection can be quite effective (Table 8) implying that farmers possess a considerable amount of knowledge which is almost totally neglected in formal plant breeding programs.

A formal plant breeding program could combine the concept of a positive use of GxE interactions with the utilization of farmers' knowledge by evaluating a wide range of germplasm under farmers' field conditions and in conjunction with farmers (Fig. 4b). In those communities where extension services and conventional seed production systems are not able to reach subsistence farmers, and farmers traditionally use their own seed from one cropping season to another, this will provide a direct link between formal plant breeding and farmers. The benefit to the farmers will be a direct access to improved germplasm. The benefit to all the community will be the maintenance of genetic diversity within a crop because different farmers are likely to select different materials.

Eventually, the formal breeding programs could become much more efficient in generating future germplasm by incorporating those selection criteria revealed during the participatory phase.

Conclusions

Breeding for marginal environments has traditionally consisted of selecting under favorable conditions. Very little breeding work for marginal environments includes selection of parents and segregating populations in environments climatically and agronomically similar to farmers' conditions.

Scientists from developing countries have been trained on breeding methods and philosophies which have been successfully used in favorable conditions. As a consequence, in most developing countries experiment stations are concentrated in the most favorable environments. The few which are in marginal environments are managed according to "recommended" agronomic practices and yield levels are much higher than in farmers' fields.

Both theory and experimental data show that this type of breeding has a low probability of success in unfavorable conditions because of GxE interactions. But, instead of recognizing that it is possible to make use of GxE interactions by breeding for specific adaptation, it has often been concluded that breeding for conditions below the crossover point is not possible. Therefore, it is usually recommended that, when the same crop is grown both in favorable and marginal conditions, breeding efforts should concentrate on the areas with favorable conditions. At the country level, larger increases of national production can be obtained by increasing production in good environments through the joint effect of improved cultivars and improved agronomic practices. However, such a strategy will neglect many small and poor farmers who could represent the majority of the farmers in the country. We believe it is possible to increase agricultural production at the country level and, at the same time, to serve small, resource-poor farmers by recognizing that the two types of environments need separate breeding programs, with different objectives, methodologies and type of germplasm.

In the case of a typical crop of unfavorable and unpredictable environments such as barley in the semiarid areas of Syria, it is possible to improve yield without additional inputs in this type of unfavorable environments under farmers' conditions. The key elements are direct selection in the

target environments and the use of locally adapted germplasm, i.e. breeding for specific adaptation. The cultivars we have developed for this type of unfavorable environments are not expected to be of interest anywhere else, but the methodology employed for their development could be useful for other types of unfavorable environments.

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Table 1. Average grain yield (t ha⁻¹) and rainfall (mm) in ten cropping seasons at the lowest and highest yielding site used in ICARDA's barley breeding program

YEAR ^a	No. of lines	Low Yielding Site		High Yielding Site	
		Grain yield (t ha ⁻¹)	Rainfall (mm)	Grain yield (t ha ⁻¹)	Rainfall (mm)
1985	168	0.743	173	3.489	373
1986	160	1.137	180	4.007	316
1987	400	.671	164	2.655	343
1988	332	2.910	382	4.420	499
1989	300	.687 6	184	5.824	214
1990	280	.471	183	3.346	317
1991	200	1.051	207	4.717	559
1992	180	.902	223	4.627	321
1993	224	0.534	221	3.671	277
1994	114	1.302	245	2.983	373
Means		1.041		3.974	

^a year of harvest

Table 2. Average grain yield (t ha⁻¹) and s.e. of the 5% highest yielding lines in the lowest yielding site (GL), and of the 5% highest yielding lines in the highest yielding site (GH), in the lowest and highest yielding sites shown in Table 1, respectively.

YEAR	in LYE		HYE		
	GL	GH	GL	GH	
1985	1.283	.767	3.462	4.139	
1986	1.935	1.340	4.139	4.970	
1987	1.076	.633	2.687	3.547	
1988	4.199	3.383	4.672	6.100	
1989	1.287	.658	4.874	7.814	
1990	.794	.429	3.066	4.122	
1991	1.693	.953	4.705	6.073	
1992	1.305	1.030	4.799	5.793	
1993	.851	.531	3.769	4.074	
1994	1.702	1.377	3.210	3.663	7
Means	1.613	1.110	3.938	5.030	

Table 3. Heritability estimates of grain yield at low- and high yield levels in different crops (from Ceccarelli, 1994).

Crop	High	Low	Reference
Cocksfoot	.89	.50	Breese, 1969
Maize	.52	.71	Selmani and Wassom, 1993
Wheat	.78	.32	Allen et al., 1978
Soybeans	.56	.31	Allen et al., 1978
Barley	.47	.54	Allen et al., 1978
Oats	.56	.63	Allen et al., 1978
Flax	.44	.56	Allen et al., 1978
Barley	.65	.66	Weltzien and Fischbeck, 1990
Oats	.38	.52	Johnson and Frey, 1967
Oats	.67	.32	Atlin and Frey, 1990
Wheat	.89	.74	Pfeiffer, 1988
Wheat	.25	.03	Roy and Murty, 1970
Wheat	.33	.68	Pederson and Rathjen, 1981
Barley	.47	.68	Singh and Ceccarelli, 1995
Oats	.45	.32	Frey, 1964

Table 4. Heritability estimates in wheat. The data are the more extremes values from a set of 31 trials conducted in 9 locations over 5 years (modified from: Pederson and Rathjen, 1981).

Grain yield (t ha ⁻¹)	Heritability
4.96	.38
3.67	.41
3.20	.00
1.04	.64
0.68	.41
0.59	.00
0.58	.43

Table 5. Mean and range of grain yield (t ha⁻¹) under stress (YS) and grain yield under non-stress (YNS) of barley breeding lines derived from Syrian landraces and of breeding lines unrelated to Syrian landraces (Non-landraces)

Set	Type of germplasm	N ^a	YS ^b		YNS ^c	
			Mean	Range	Mean	Range
1	Non-landraces	155	.488	0.000-0.893	3.901	2.310-4.981
	Landraces ^d	77	.788	0.486-1.076	3.413	2.398-4.610
2	Non-landraces	207	.589	0.197-1.101	5.400	3.558-6.962
	Landraces	43	.734	0.468-0.954	4.435	2.883-5.728
3	Non-landraces	296	.634	0.000-1.119	2.687	1.241-3.893
	Landraces	83	.802	0.414-1.203	2.513	1.829-3.738
4	Non-landraces	165	.525	0.196-0.852	3.631	1.339-4.862
	Landraces	76	.764	0.567-0.990	3.275	1.378-4.309

^a Number of lines

^b YS = average grain yield in location-year combinations with average yield lower than the means of all testing sites minus one standard deviation

^c YNS = average grain yield in location-year combinations with average yield higher than the means of all testing sites plus one standard deviation

^d pure lines obtained by pure line selection within landraces

Table 6. Mean and range of yield in unfavorable conditions (means of 5 sites with mean yields of .354, .566, .732, .859 and 1.155 t ha⁻¹, respectively) of three groups of barley lines selected in unfavorable and in favorable (YP1, YP2, YP3) conditions

Material ^a	Mean	Range	YD/YP ^b	TOPYD/TOPYP ^b	TOP line/check ^b
YD1	.737	.596-.798	1.46	1.19	0.88
YP1	.506	.257-.668			0.74
YD2	.804	.585-.909	1.25	1.06	1.01
YP2	.643	.481-.755			0.84
YD3	.948	.870-1.052	1.28	1.13	1.17
YP3	.738	.606-.846			0.94
Best check	.903				

^a YD1, YD2 and YD3 indicate barley lines selected in unfavorable conditions in the three periods 1986-88, 1987-1989 and 1988-1990, respectively, whilst YP1, YP2 and YP3 indicate barley lines selected in favorable conditions in the same periods as the corresponding YD lines.

^b The three ratios indicate the average yield advantage of YD lines over YP lines (YD/YP), the yield advantage of the best YD line over the best YP line (TOPYD/TOPYP), and the yield advantage of the best YD and YP line over the best check (TOP line/check), respectively.

Table 7. Number (No) and percent (%) of lines selected in Syria and in Maghreb countries (Libya, Tunisia, Algeria and Morocco) from a common nursery of 288 lines

Selected in:	No	% ^a
Syria	103	35.8
Maghreb	154	53.5
Syria and Maghreb	49	17.0
Syria-discarded in Maghreb	54	52.4
Maghreb-discarded in Syria	105	68.2

^a the first three percentages are calculated on the total number of lines (288) in the nursery, the last two are calculated on the number of lines selected in Syria and Maghreb, respectively.

Table 8. On-farm performance of varieties of bush bean selected from on-station trials by farmers and of varieties selected by breeders in Rwanda (modified from Sperling *et al.*, 1993)

Year	Number of trials	% of trials where new variety outyielded local mixture	Yield increase (%) of new variety over local mixture
FARMER SELECTION			
1989	11	73 ns	3.9 ns
1989	19	89 **	33.4**
1990	36	64 ns	12.9 ns
1990	18	83 **	38.0*
BREEDER SELECTION			
1987	32	34 ns	-8.8 ns
1988	45	49 ns	-18.9 ns
1988	15	53 ns	0.7 ns

*, ** differences significant at $P < 0.05$ and $P < 0.01$, respectively; ns, not significant

LEGEND OF FIGURES

- Fig. 1. Cumulative probability of barley yields in two climatic zones of Syria (zone C receiving less than 250 mm annual rainfall, and zone B receiving 250-350 mm annual rainfall) between 1983 and 1994. The distributions are based on 72 and 101 location-year combinations for zone C and B, respectively.
- Fig. 2. An example of crossover type of GxE interaction in barley: YP and YD are lines selected in high and low yielding environments, respectively and then tested in 21 location-year combinations. On the X-axis the location-year combinations are combined in five groups according to the average grain yield of 64 barley lines. The two lowest and the two highest yielding groups are representative of farmers' fields and of experiment stations, respectively.
- Fig. 3. Relationships between heritability and yield in two sorghum populations (modified from Zavala-Garcia *et al.*, 1992).

Fig. 4. Formal (a) and participatory (b) breeding programs: in a formal breeding program farmers are passive recipients, in the second they participate in the development of new cultivars.