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Summary

Many areas of world, particular those where agriculture is largely practiced by resource-poor farmers with little or no use of external inputs, have not benefitted from the spectacular yield increases achieved by the combination of modern breeding technologies and use of inputs. The paper argues that because breeding is mostly conducted in presence of high inputs, it has systematically missed the opportunity to exploit genetic differences at low levels of inputs. Many studies show that these differences do exist, particularly in the case of fertilizers, and that these differences can only be identified is selection is conducted under the target level of inputs. Although this was predicted by theory more than 40 years ago, and has been supported by a large body of experimental data, very few breeders select in sub-optimal or stress conditions. The most common justification is the high environmental variation, and hence the lower heritability expected in low input conditions. While this is not supported by experimental evidence, the paper shows that in the case of a typical crop grown in low-input and climatically marginal conditions such as barley, genetic gains are possible by using locally adapted germplasm and by selecting in the target environment. Similar conclusions, in relation to the use of a low-input selection environment, have been reached recently in maize. It is concluded that the best avenue to a sustainable increase of agricultural production in low-input agricultural systems is through locally based breeding programs.

Introduction

Adaptation to low/high input cultivation will be discussed throughout this paper in an agronomic, rather than in a biological context. Hence, a genotype, or breeding line, or cultivar will be considered adapted to a given type of conditions (climatic, agronomic, edaphic) when it is able to give an economic production, and not necessarily only survives in that set of conditions. This recognizes that there could be adaptation without economic productivity, but not economic productivity without adaptation.

Adaptation of agricultural crops to their environment has been a key factor to the yield increases which have occurred since the spread of crops to new environments (Evans, 1980). From the early stages of domestication most of the selection was by farmers for better adaptation to very specific environments (Bramel-Cox et al., 1991). Beginning towards the end of the last century, the agricultural environment began to be modified, first by the use of fertilizers, later by the use of pesticides, fungicides and herbicides. The process of adapting crops to gradually changing agronomic conditions has become more efficient through the use of systematic breeding programs, and selection by breeders has been for high yield potential and broad adaptation. Therefore, the consequent yield increases have been achieved as a combined effect of an agronomic environment made more favorable for plant growth and of cultivars better adapted to that environment.

It has been estimated that the spectacular yield increases of crops during the second part of this century have to be attributed in almost equal measure to breeding and to the use of inputs. These yield increases have occurred in most of the crops in most of the developed countries but only in some crops in some developing countries. Large areas of Africa, Central and South America, and Asia have been by-passed by the high-

Table 1. Average grain yield (kg ha^{-1}) of the ICARDA Barley Regional Yield Trials for low- and high-rainfall areas (1985–1991) conducted on research stations and national average yields in a number of countries

Country	Average yield in exp. stations		National average yield
	Low rainfall trials	High rainfall trials	
Algeria	2993	4168	862
Afghanistan	1565	3462	1070
China	5349	3890	2836
Cyprus	3160	4804	1948
Egypt	2798	3855	2698
Ethiopia	1690	3042	1131
Iran	2782	3597	1143
Iraq	945	819	741
Jordan	2294	2820	684
Lebanon	2319	2828	1884
Libya	1465	2886	596
Morocco	2926	3715	1140
Pakistan	1897	2275	772
S. arabia	6610	4280	3887
Syria	3417	3367	716
Tunisia	3261	3883	735
Turkey	2077	3635	2043

input type of agricultural development (Maurya et al., 1988; Haugerud & Collinson, 1990; Pimbert, 1994). Despite the large benefits obtained, the use (or perhaps the abuse) of agricultural inputs – not only chemicals but also water – has caused an increasing concern for the environmental consequences of a strategy based on modifying the environments to fit crops and varieties with an increasing yield potential – a strategy that may be not sustainable in the long term (Poutala et al., 1994). Environmental degradation, abuse of physical resources (mostly water and soil) and of biological resources have become an international concern during the last ten years, and terms such as sustainability, friendly or ecological or biological agriculture, and similar, have become part of the every-day jargon of agricultural scientists and administrators.

The debate is often polarized between scientists advocating a 'clean agriculture' and scientists concerned with feeding a growing population, and it is best summarized in the following joint statement by the U.S. National Academy of Sciences and the U.K. Royal Society: 'If current predictions of population growth prove accurate and patterns of human activity on the planet remain unchanged, science and technology may not be able to prevent either irreversible degradation of the environment or continued poverty for much of the world' (Norse, 1992). Although this issue provides a general framework for discussing adaptation to low/high inputs, this paper will address the more specific question of why the adaptation to increasing levels of inputs, which has been a constant objective in modern plant breeding, did not have beneficial effects in those traditional agricultural systems which are characterized by harsh environments and limited use of external inputs. It has been estimated that some 1.4 billion people are dependent on this type of agriculture (Pimbert, 1994) and that resource-poor farmers practice approximately 60% of global agriculture, and produce 15–20% of the world food (Francis, 1986). These farmers have never known the Green Revolution.

Institutional breeding and low-input agriculture

Although there are as many different ways of running a breeding program as there are breeders, most breeding programs, both in developed and in developing countries, share some general concepts and, consequently, some common ways of handling breeding materials.

Some examples of what most breeders commonly do are: (a) selection is conducted in research stations with optimum amount of fertilizers, weed control and water supply, often in crop rotations that little have in common with reality (Rathjen & Pederson, 1986; Atlin & Frey, 1989a, 1989b; Simmonds, 1991). This is done because under these conditions environmental noises can be kept under control, error variances are small, and response to selection high; (b) breed cultivars that are genetically homogenous (pure lines, hybrids, clones) to fit the rules for variety registration which in many developing countries are as strict as in developed countries; (c) new varieties are released based on their average performance in trials conducted for a number of years and in a number of locations, often at near-optimum levels of crop management (some breeding programs in Australia are an exception); (d) in developing countries locally adapted landraces are seen as one of the reasons for low yield and therefore they must be replaced; (e) seed of improved varieties is made available to farmers through mechanisms and institutions such as variety release committees, seed certification schemes and seed production organizations; (f) the end users of new varieties are not involved in selection and testing; they are only involved at the end of the consolidated routine (breeding, researcher managed trials, verification trials), to verify if the choices made for them by others are appropriate or not.

Breeding programs based on this set of concepts have been very efficient in developed countries, and in general in environments which are either favorable or which can be made favorable by the use of external inputs. This is because the agronomic and climatic conditions in farmers' fields and in the experiment station are not very different from each other. Therefore genotype × environment interaction is unlikely to pose major problems. Uniformity of varieties is needed to meet the requirements of a market-oriented agriculture, broadly adapted varieties fit the requirements of the seed industry, seed distribution mechanisms are efficient and new varieties can quickly reach the farmers.

Agriculture in many developing countries, and particularly in unfavorable conditions, offers a very different picture.

Yield levels in farmers' fields are often several fold lower than those obtained in research stations. An example is given in Table 1 for a crop such as barley which is traditionally grown in unfavorable conditions. Low yields in farmers' fields are often due to low levels of inputs (particularly fertilizers, herbicides and pesticides), but also to what researchers consider inappropriate time of sowing, poor soil preparation, in general poor agronomic techniques. These 'primitive' agronomic practices are only partly due to the ignorance of farmers as too often it is said. Fertilizers, herbicides and pesticides are often not unknown to farmers, but they are either not available or too expensive, or their use is perceived by farmers as risky in an environment with a high probability of crop losses due to climatic event such as drought (McDonald, 1989). Herbicides may not be used because what an agricultural scientist considers a weed is often seen by a farmer as a source of animal feed, and what the same agricultural scientist defines as "hand weeding" is often "harvesting a forage crop". The yield advantage of changing sowing date or the phenology of the crop can be easily demonstrated on research stations and that particular technology ends in an Annual Report as a 'recommended practice'. Farmers, particularly small and resource-poor farmers, often have to seek off-farm sources of income which can prevent them from changing a number of operations on the farms and which can be much greater than those derived from the 'recommended' agricultural practices. Demonstrating the benefit of an appropriate and timely seed-bed preparation is too often purely academic because obtained in the experiment station with machinery acquired through development aids and available nowhere else in the country.

Resource-poor farmers in many regions of the word practicing agriculture in these situations have adopted a strategy based on both intraspecific and interspecific diversity (Martin & Adams, 1987). A number of different crops are usually grown in the same field at the same time (intraspecific diversity), and the cultivars of the different crops are usually genetically heterogeneous (interspecific diversity). A second level of interspecific diversity is obtained by growing, at the same time and in the same field, different cultivars of the same crops (Haugerud & Collinson, 1990). The type of diversity which prevails in different areas depends on both climatic and socioeconomic conditions. In central Africa and central America both intra- and interspecific diversity are exploited at the same time. In other areas, interspecific diversity represented by one heterogeneous cultivar, is predominant. In the dry areas of West Asia and North Africa, for example, barley is often the only possible rainfed crop, and the cultivars which are grown at present, and which have been grown for centuries, are genetically heterogeneous (Ceccarelli et al., 1987; Weltzien & Fischbeck, 1990).

While the typical concepts of institutional breeding listed earlier seem to fit well advanced agricultural systems, they seem to be in a sharp contrast with the realities of low-input agriculture practiced by resource-poor farmers. The rest of the paper will discuss in details two of these concepts, namely the environment where selection is conducted and the type of germplasm, in relation to adaptation to high/low input conditions. Before doing that it may be useful to clarify that low/high input cultivation means different things in different countries. In high-input agricultural systems low-input cultivation is seen as one way of responding to environmental concerns. In low-input agricultural systems low-input agriculture, as practiced by resource-poor farmers, is not an option but in the majority of cases is dictated by the physical and economic environment. In this case adapting crops to low-input cultivation is the only avenue to increase agricultural production in the short term.

Selection environment and adaptation

The theoretical framework of this issue, which essentially is a case of Genotype × Environment (G × E) Interaction and which continues to be hotly debated among plant breeders, has been developed by Falconer more than 40 years ago (Falconer, 1952). A recent review of experiments, mostly on animals (Falconer, 1990), showed that 'If a breeder wants to improve performance in environment A he should select in environment A' (see also Falconer, 1993). The conclusions of Falconer have been confirmed by theoretical studies such as those of Rosielle & Hamblin (1981) and Simmonds (1991), and are supported by experimental data on both self-pollinated and cross-pollinated crops (reviewed by Ceccarelli, 1994) and on small ruminants (reviewed by Bradford & Berger, 1988).

An example of this type of experimental data is shown in Figure 1 with data from barley in Syria. 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 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 cross-over. These data, like others published earlier (Ceccarelli & Grando, 1991a, 1991b; van Oosterom et al., 1993), indicate that the top yielding lines a breeder selects in a high yielding environment (high inputs and favorable climatic conditions) would not be selected in a low yielding environment (low inputs and unfavorable climatic conditions, and viceversa. The implications of the data in Figure 1 are clearer by considering the cumulative probability distribution of grain yield of barley in two agroecological zones of Syria (Figure 2). In the drier areas (where the use of inputs is limited by the high frequency of abiotic stresses) the probability of yields less than 1.5 t ha^{-1} is about six times higher than the probability of yields exceeding 3 t ha^{-1}. Therefore, the lower yield potential of the YD lines, specifically selected for the most frequent type of conditions is not a serious problem.

The majority of experimental data indicating a G × E interaction of cross-over type are from studies where the environment is characterized by the mean yield of the lines under testing, and low- and high-yielding environments are not related to specific climatic or edaphic causes. However, most of the studies which

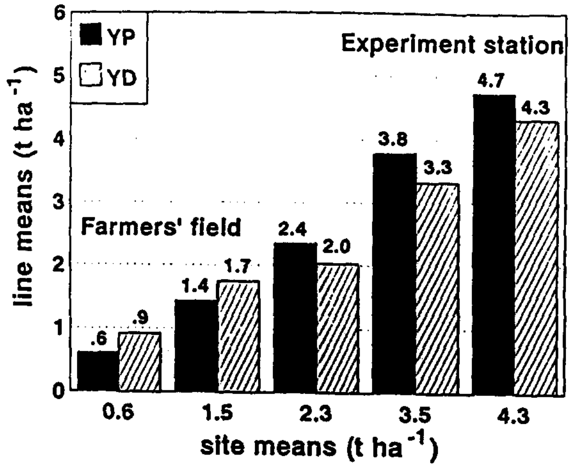

Figure 1. An example of cross-over type of G × E interaction in barley: YP and YD are lines selected in high and low yielding environments, respectively and then tested in 21 location-year combinations. On the X-axis the location-year combinations are combined in five groups according to the average grain yield of 64 barley lines. The two lowest and the two highest yielding groups are representative of framers' fields and of research stations, respectively.

Table 2. Grain yield (t ha^{-1}) of two barley cultivars in Sardinia with standard agronomic practices (weed control and 80 kg ha^{-1} of N) and with reduced inputs (no weed control and 40 kg ha^{-1} of N) (from: Attene et al., in press)

Cultivar	Grain yield[a]	
	weed control and 80 kg ha^{-1} of N	no weed control and 40 kg ha^{-1} of N
Formula	6.3a	3.6b
Local landrace	5.4b	4.3a

[a] Values followed by different letters are significantly different at $P < 0.05$.

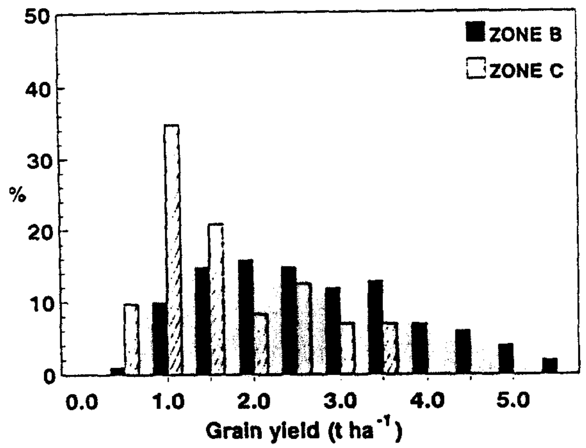

Figure 2. Frequency distribution of barley yields in two climatic zones of Syria (zone C receiving less than 250–300 mm annual rainfall, and zone B receiving 300–350 mm annual rainfall) between 1983 and 1994. The distributions are based on 72 and 101 location-year combinations for zone C and B, respectively.

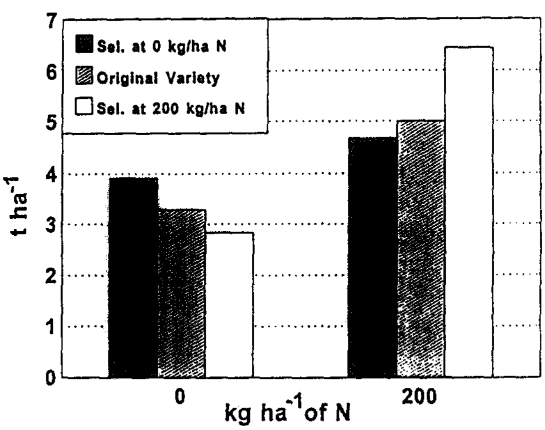

Figure 3. Grain yield, at 0 and 200 kg/ha of N, of an open pollinated maize population, and of two synthetics developed from the ten highest or the ten lowest yielding half-sib progenies at 0 and 200 kg/ha of N (from Muruli & Paulsen, 1981).

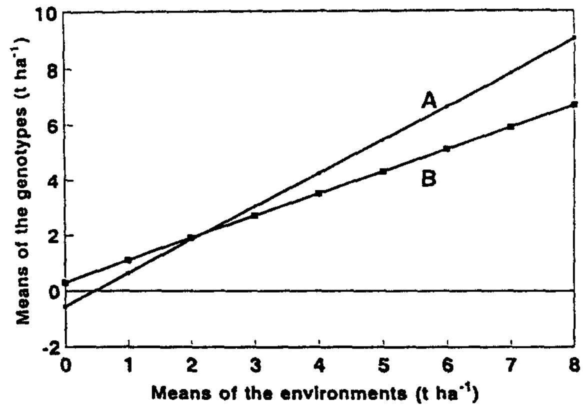

Figure 4. Cross-over type of G × E interaction: A and B are typical genotypes selected in high and low yielding environments, respectively (redrawn from Simmonds, 1984).

deal with genotypic responses to specific inputs show a similar pattern of responses. Balko & Russell (1980) found a strong genotype × nitrogen level interaction in maize, and Muruli & Paulsen (1981) showed that it is possible to obtain response to selection conducted in a low-nitrogen environment (Figure 3). This suggests that the alleles controlling yield in the low- and high-nitrogen level are not identical. Similarly Atlin & Frey (1989a) found genotype × phosphate interaction in oats, predicting that direct selection at low-P levels was superior to indirect selection, i.e. selection at high P-levels. However, no interaction was found with nitrogen levels. Other examples of interaction between genotypes and fertilizer levels (nitrogen, phosphate and potash) in oats, barley, white clover, sorghum, common bean and tomato are given by Atlin & Frey (1989b). Recently Attene et al. (1995) showed an example of genotype × agronomic practices (nitrogen fertilizer and weed control) interactions in barley (Table 2).

The frequency with which genotype × input interactions occur indicates that alleles that confer specific adaptation to low-input conditions may exist in many crop species (Atlin & Frey, 1989b).

These results are not surprising in the light of a review of plant productivity in relation to nutrients, types of management and stresses published in 1982 (Boyer, 1982). The review concludes 1) that there are genetic differences in the ability of plants to accumulate nutrients such as iron, nitrogen, phosphorus and a number of micronutrient, and 2) that 'considerable success can be expected if plant improvement includes selection under conditions that are often unfavorable for growth. . . so that genotypes capable of exploiting limited resources can be identified. With these genotypes, large scale modifications of the environment is less necessary'.

If we broadly define as stress environments those environments where plant productivity is limited by either climatic or nutritional factors, these results also agree with the circumstantial evidence that plant breeding has not been as effective in stress environments as it has been in optimum or near-optimum environments

(Maurya et al., 1988; Haugerud & Collinson, 1990; Jansen et al., 1990; Grisley & Shamambo, 1993; Sperling et al., 1993; Hardon & de Boef, 1993).

The experimental data discussed so far can be summarized schematically as in Figure 4 which shows the environmental response of hypothetical genotypes selected under high (A) and low (B) input conditions (or in a high- and low-yielding environment). The figure, first published by Simmonds (1984) indicates that, in general, genotypes selected for adaptation and performance in high input conditions, are not well adapted to low input conditions. The question of whether the same genotype can be equally well adapted to high and low yield levels, caused by different levels of climatic or nutritional stresses, is hotly debated among breeders while some animal and plant geneticists (Allard & Hansche, 1964; Falconer, 1990) and plant physiologists (Evans & Wardlaw, 1976; Fischer & Maurer, 1978; Fischer & Wood, 1979; Blum, 1993) have long since recognized that species and varieties adapted to favorable growing conditions are, in general, not well adapted to stress conditions.

A number of studies did not reveal the presence of cross-over interactions (Castleberry et al., 1984; Austin et al., 1989; Khan & Spilde, 1992; Bulman et al., 1993) but indicated that rates of gain in yield from genetic improvement are smaller or even nonexistent in low input or stress environments as compared to high input, highly productive conditions (Smith et al., 1990). These studies do not necessarily contradict those showing the presence of cross-over interactions.

Besides the experimental difficulties of comparing old and modern varieties, the comparison which is missing in these studies is between cultivars specifically selected for high-input cultivation and cultivars specifically selected by modern breeding for low-input cultivation.

Most of the evidence would therefore suggest that 1) in most crops there is genetic variation for adaptation, and hence yield, in low-input conditions, 2) that the most efficient way to improve adaptation and yield in low-input conditions is by direct selection in low-input conditions.

Selection in low input conditions

Despite the evidence given above, very few breeding programs conduct early generation selection in low input, and more in general, in stress conditions. The most common justification given for this widespread reluctance is low heritability. The justification is largely groundless. Firstly, theory of indirect selection shows that response to selection done in a different environment is a function of not only heritability but also of the genetic correlation coefficient between the selected trait measured in the two environments (Falconer, 1989). Secondly, the evidence that heritability in stress environments is lower than in non-stress environments is not as obvious as many breeders claim (Table 3). Furthermore there have been many reports that narrow sense heritability increases in response to increased environmental stresses (Ward, 1994). This agrees with a cross-over type of genotype × environment interactions (Figure 4), where the lowest heritability is expected at the cross-over point and explains some of the disagreement among breeders on the issue of the optimum environment of selection.

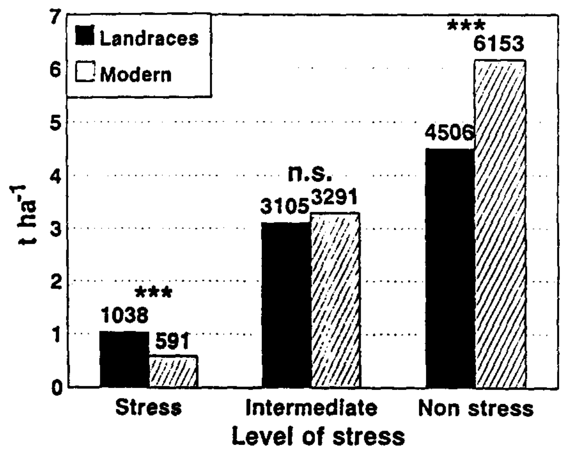

Figure 5. Differences in grain yield between modern barley cultivars and Syrian barley landraces at three different yield levels. (n.s. = non significant, *** significant at $P < 0.001$ based on t-test for groups of unequal size).

When the target environments lie above the cross-over point the best discrimination between breeding lines occurs in the highest yielding environments. In the lowest yielding environments (close to the cross-over point) breeding lines tend to look alike, hence the low heritability which is often found. When the target environments lie below the cross-over point, the largest differences between genotypes are found at the lowest yield levels and the identification of the best genotypes becomes increasingly difficult as yield levels increase. An example is given in Figure 5 where 44 pure lines from Syrian barley landraces and 206 modern barley cultivars are compared at three levels of

Table 3. Heritability estimates of grain yield at low- and high yield levels and ratio between the root squares of the two heritabilities in different crops (modified from Ceccarelli, 1994)

Crop	High (h_y)	Low (h_x)	Ratio h_y/h_x	Reference
Wheat	0.33	0.68	0.70	Pederson & Rathjen, 1981
Barley	0.47	0.68	0.83	Singh & Ceccarelli, 1995
Oats	0.38	0.52	0.85	Johnson & Frey, 1967
Maize	0.52	0.71	0.86	Selmani & Wassom, 1993
Flax	0.44	0.56	0.89	Allen et al., 1978
Maize	0.46	0.58	0.89	Lafitte & Edmeades, 1994
Barley	0.47	0.54	0.93	Allen et al., 1978
Oats	0.56	0.63	0.94	Allen et al., 1978
Barley	0.65	0.66	0.99	Weltzien & Fischbeck, 1990
Wheat	0.89	0.74	1.10	Pfeiffer, 1988
Oats	0.45	0.32	1.18	Frey, 1964
Sorghum	0.63	0.43	1.21	Zavala-Garcia et al., 1992
Cocksfoot	0.89	0.50	1.33	Breese, 1969
Soybeans	0.56	0.31	1.34	Allen et al., 1978
Oats	0.67	0.32	1.45	Atlin & Frey, 1990
Sorghum	0.69	0.32	1.47	Zavala-Garcia et al., 1992
Wheat	0.78	0.32	1.56	Allen et al., 1978
Wheat	0.25	0.03	2.89	Roy & Murty, 1970

Table 4. Grain yield (mean, standard error and range in kg ha^{-1}) of Syrian barley landraces and of modern cultivars in low and high yielding locations. The number of landraces was 44 and 76 and the number of modern cultivars was 206 and 165 in the first and second set, respectively

Location/year[a]	Rainfall (mm)	Landraces		Non landraces	
		Mean ± s.e.	Range	Mean ± s.e.	Range
First set					
Bouider, 1989	186	1038 ± 25.4	790–1479	591 ± 16.7	0–1364
Athalassa, 1989	344	4506 ± 114.6	3003–6316	6153 ± 60.3	3509–8820
Days to heading		120 ± 0.3		118 ± 0.2	
Second set					
Breda, 1990	185	610 ± 4.9	302– 918	388 ± 10.9	0–747
Tel Hadya, 1988	504	3611 ± 16.2	1326–6190	5126 ± 97.1	1580–7852
Days to heading		115 ± 0.8		113 ± 0.3	

[a] Bouider, Breda and Tel Hadya are three selection and testing sites in northern Syria: in Bouider and Breda no inputs were used. In Tel Hadya and Athalassa (Cyprus) both nitrogen (60 kg ha^{-1}), phosphate (50 kg ha^{-1}) and weed control were applied.

stress resulting from different amounts of inputs and different rainfall. At the lowest and highest yield levels there were significant differences between the two groups of germplasm, while the difference was not significant at the intermediate level, near to the cross-over point.

The data of Figure 5 raise the issue of whether the type of cultivars developed by breeding in high-inputs and climatically favorable conditions, is the best genetic material to test the potential of low-input conditions.

In many developing countries, and for crops grown in low-input conditions and in stress environments, landraces are still the backbone of agricultural production. The reasons why farmers prefer to grow only landraces or continue to grow landraces even after partial adoption of modern cultivars are not well documented. Food and feed quality and seed storability are often quoted as common reasons for this preference, but also important is the belief that landraces are able to produce some yield even in difficult conditions where modern vari-

Table 5. Average increase in grain yield (kg ha^{-1}) over local landraces of three barley lines obtained through pure-line selection from the two landraces commonly grown in Syria. The data are from on-farm trials

Line	Nr. of environments[a]	Grain yield	% increase
Arta	51	2433	22.3
Tadmor	11	780	23.6
Zanbaka	8	945	22.4

[a] Location-year combinations.

Table 6. Grain yield (t ha^{-1}) at low (N-) and high (N+) nitrogen level of experimental maize cultivars selected for high grain yield at either low or high nitrogen level (modified from: Lafitte & Edmeades, 1994)

Testing conditions	Selected for	
	Grain yield at N+	Grain yield at N-
N-	1.89	2.22
N+	6.20	5.70

eties are less reliable. This is in fact the case in those areas where farmers have adopted modern cultivars but have kept the landraces in the most unfavorable areas of the farm.

To illustrate the value of this type of germplasm I will use the example of barley in Syria. Barley landraces are still the predominant cultivars in countries such as Ethiopia, Eritrea, Nepal, Yemen, and in all the Middle East and large areas of North Africa. In Syria, barley production is entirely based on two landraces, Arabi Abiad (white seed) and Arabi Aswad (black seed). The first is common in slightly better environments (between 250 and 400 mm rainfall) and the second in harsher environments (less than 250 mm rainfall) – a clear example that farmers recognize the value of specific adaptation.

About 10 years ago pure lines extracted from Syrian barley landraces began to be routinely evaluated in the breeding program at ICARDA. Therefore it has been possible to compare landraces and modern cultivars in a range of conditions ranging from severe stress (low-input and low rainfall) to moderately favorable conditions (use of inputs and high rainfall). These comparisons (such as the example shown in Table 4) have consistently indicated that 1) landraces, as a group, yield more than modern cultivars under low-input and stress conditions, 2) the superiority of landraces is not associated with escape mechanisms as shown by heading date; 3) within landraces there is considerable variation for grain yield under low-input and stress conditions, but all the landraces-lines yield something whereas some modern cultivars fail; 4) landraces are responsive to both inputs and rainfall and the yield potential of some lines is high, though not as high as modern cultivars, and 5) 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. The data of Table 4 indicate that selection conducted only in high-input conditions is likely to miss most of the lines that would have performed well under low-input conditions.

The adaptation of landraces to the physical environment in which they evolved, coupled with the genetic diversity they harbor, suggests that pure-line selection within landraces conducted in the target environment could be a promising avenue for short terms gains. Indeed the combined use of the target environment for selection and of locally adapted germplasm has generated lines which outyield the local landraces by more than 20% in farmers' fields (Table 5). A longer term approach is the use of selected lines from landraces to reconstitute mixtures with the objective of using population buffering to stabilize production over time.

A recent example of breeding progress with direct selection in low-input conditions is in maize where a divergent selection experiment (Table 6) showed that the largest grain yields at low soil nitrogen levels were obtained from direct selection at low soil nitrogen levels (Lafitte & Edmeades, 1994), thus confirming the role of the selection environment.

Breeding in variable, unpredictable, low yielding conditions is with no doubts much more difficult than breeding in the uniform, predictable, fully controlled, highly productive conditions of the experiment station. Plot techniques and experimental designs which work well in the experiment station are usually unsuited to control environmental variability in low-input conditions. It has been shown elsewhere that a sufficient degree of precision (in experimental terms) can be obtained in conditions which are often considered, *a priori*, unsuitable to breeding work when innovative experimental techniques are used (Ceccarelli & Grando, 1996).

Not by grain alone

Adaptation to low-input cultivation, particularly in third word countries, requires a full understanding of

Table 7. Grain yield (kg/ha^{-1}), plant height (cm) and harvest index in stress (low rainfall and no fertilizer) and no stress (high rainfall and addition of phosphate) of barley lines with the highest grain yield in stress (HYS) and non stress (HYP) conditions

Trait	HYP	HYS	Difference
	Mean ± s.e.	Mean ± s.e.	
Grain yield – no stress	3577 ± 62	2822 ± 64	755***
Grain yield – stress	745 ± 49	1096 ± 74	- 351***
Plant height – no stress	62 ± 2	58 ± 1	4 n.s.
Plant height – stress	29 ± 0.6	30 ± 0.5	- 1 n.s.
Harvest index – no stress	0.46 ± 0.02	0.37 ± 0.02	0.09***
Harvest index - Stress	0.27 ± 0.02	0.40 ± 0.01	- 0.13***

n.s. = non significant; *** significant at P < 0.001.

Table 8. Grain yield (kg/ha(cm) and harvest index in stress (low rainfall and no fertilizer) and no stress (high rainfall and addition of phosphate) of Syrian barley landraces and of modern cultivars with similar phenology

Trait	Landraces	Modern	Difference
	Mean ± s.e.	Mean ± s.e.	
Grain yield – no stress	3596 ± 114	3749 ± 147	- 153 n.s.
Grain yield – stress	1198 ± 78	489 ± 66	709***
Plant height – no stress	69 ± 1	67 ± 3	2 n.s.
Plant height – stress	29 ± 1	27 ± 1	2 n.s.
Harvest index – no stress	0.48 ± 0.03	0.51 ± 0.03	-0.03 n.s.
Harvest index – stress	0.42 ± 0.01	0.22 ± 0.03	0.20***
Lodging % – no stress	100	0	100***
Lodging % – stress	0	0	0 n.s.
Days to heading	105 ± 0.4	106 ± 2.0	1 n.s.

n.s. = non significant; *** significant at P < 0.001.

the role and utilization of different crops in a given system. The example of plant height in cereals will be used to illustrate this general principle. One of the few issues in plant breeding where the consensus is almost unanimous is that the impressive yield increases obtained in some of the major cereal crops is associated with a higher harvest index. The introduction of dwarfing genes and stiff straw has made crops able to respond to higher fertilizer doses without lodging, thus expressing fully the higher yield potential associated with the higher harvest index. In many countries not only the grain but also the straw may have considerable value to the farmer mostly as source of animal feed. This is certainly the case of barley in West Asia, North Africa, Ethiopia, Nepal, only to mention some countries, but also the case of pearl millet, sorghum, maize, and to some an extent wheat. In many low-input agricultural systems not only the amount of straw but also its quality, particularly softness, is important both when the straw is utilized on the farm and when it is sold on the market.

In the case of barley, genotypes with high harvest index and high grain yield in high-input conditions seem unable to maintain a high harvest index when exposed to moisture and nutritional stress (Table 7). By contrast, barley genotypes specifically selected for high grain yield in low-input and moisture stress conditions have a low harvest index in high-input conditions (and consequently a low grain yield), but are able to maintain the harvest index at the same level when exposed to low-input conditions. Therefore, although a high harvest index seems to be an advantage also in low-input conditions, it can only be selected for by exposing breeding material to those conditions.

Syrian barley landraces offer an additional insight into the relationships between objectives of modern breeding and specific adaptation to the farming systems of low-input agriculture. Surprisingly, their harvest index is not extremely low in high-input conditions (Table 8), probably because of their extremely thin stems which makes them very susceptible to lodging (Ceccarelli, 1993). In low-input conditions their harvest index is only marginally reduced, they become very short and they do not lodge. Although it may sound as a paradox, it looks as if landraces express the typical traits of a high yielding cultivar in high input conditions, but only when grown under low-input and stress conditions.

Both examples show that low-input and moisture stress conditions cause invariably a reduction in plant height. The crop may become too short to be combine-harvested and farmers do not have alternatives to the costly hand-harvesting. Therefore, one of the main breeding objectives in this situation is to increase plant height under drought while keeping the straw sufficiently palatable. The consequences are inevitable: a tall crop with soft straw is precisely the opposite of what a modern breeder would be looking for.

Conclusions

The topic of this paper has been the object of a number of reviews in the last few years (for example Atlin & Frey, 1989b; Smith et al., 1990; Bramel-Cox et al., 1991). These reviews recognize that there is a general agreement on a number of points. Firstly, that the occurrence of genotype by environment interactions of cross-over type is a widespread fenomenon. Second, that in case of genotype by environment interactions, the magnitude of heritability is not a useful criterion to decide on the optimum environment where to do selection. Third, that the assessment of genetic correlation between performance under contrasting situations is essential to predict the likely impact of genotype by environment interactions. Fourth, that the magnitude and the type of genotype by environment interactions depends on how wide is the range of conditions (input levels, rainfall, soil fertility) under which a given crop is grown.

The major point of disagreement in the literature is on what to do when genotype by environment interactions of cross-over type occur. The most common view is that breeding is ineffective below the cross-over point and therefore the use of inputs is a prerequisite before embarking on plant improvement programs. By improving the agronomic environment, yields are raised above the cross-over point, and therefore selection can be conveniently done within the comfortable world of the research stations. This view is extremely popular in developing countries and produces brilliant results on research stations. It serves, but not always, the minority of farmers whose agronomic and climatic environment is not too dissimilar from the research stations.

The main conclusion of this paper is that resource-poor farmers and low-input agriculture can only be served by taking the opposite view which recognizes that breeding can be effective below the cross-over point. This view is much less popular, and consequently there are not very many examples to quote. The few which are available indicate that yield increases with varieties specifically adapted to low-input conditions, though far for being spectacular, are sufficiently high to stimulate not only adoption of the variety but also adoption of better crop husbandry. However, specific adaptation is not a very popular concept. Presumably because it does not bring the same prestige to the breeder as the concept of wide adaptation and is not in the interest of the seed industry.

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