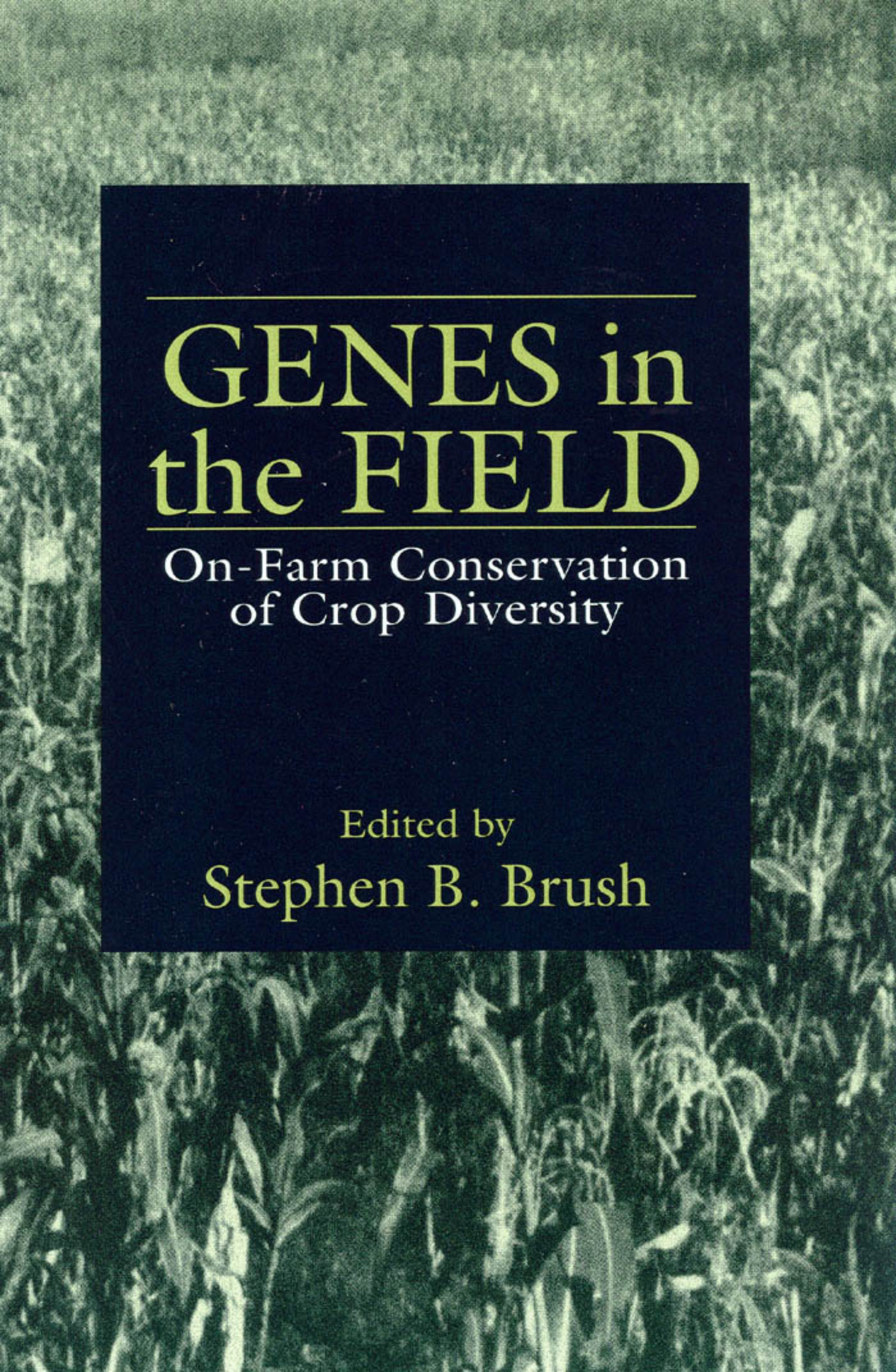

GENES in the FIELD

On-Farm Conservation of Crop Diversity

Edited by

Stephen B. Brush

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Stephen B. Brush, Ph.D.

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chapter three

Barley landraces from the Fertile Crescent: a lesson for plant breeders

Salvatore Ceccarelli and Stefania Grando

Introduction

The domestication of wheat and barley took place prior to 7000 B.C. in the region of the Near East known as the "Fertile Crescent." The Fertile Crescent includes parts of Jordan, Lebanon, Palestine, Syria, southeastern Turkey, Iraq, and western Iran (Figure 3.1). Evidence suggests that the most important of the early cereals was barley, and the archaeobotanical material from the region clearly shows that the first barleys were two-rowed (Harlan and Zohary 1966). The wild progenitor of cultivated barley, *Hordeum vulgare* ssp. *spontaneum,* is still widely distributed along the Fertile Crescent where, particularly in the driest areas, it can be easily identified from a distance because of its height. It is likely that *Hordeum spontaneum* contributes to the evolutionary processes of barley landraces through a continuous introgression of genes.

Today barley is still one of the most important cereal crops in the Fertile Crescent, spanning an area of approximately 5 million hectares. Barley is a typical crop in marginal, low-input, drought stressed environments (Ceccarelli 1984). Barley seed and straw are the most important source of feed for small ruminants, primarily sheep, and therefore palatability of straw in particular, but also of grain, is an important attribute to most farmers. Conventional breeding and high yielding varieties (HYVs) have had virtually no success in this region, which has had a positive effect on preserving biodiversity. In these environments, all cultivated barleys are landraces (Weltzien 1988) that have evolved directly from the wild progenitor. They have adapted to hostile environments and are popular among farmers for their high feed quality as both grain and straw.

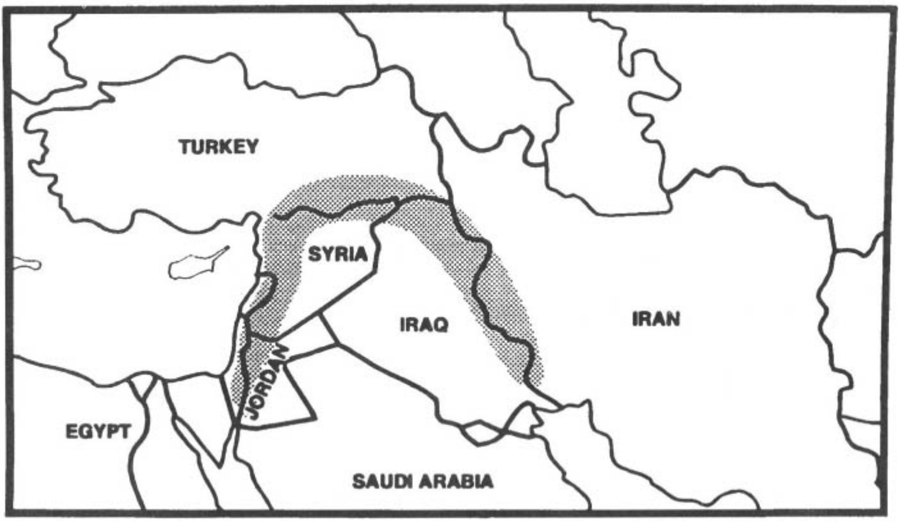

Figure 3.1 The "Fertile Crescent," where crops such as barley, wheat, lentil, stone fruits, and olives were domesticated. (Modified from Harlan and Zohary 1966.)

In Syria farmers identify two major groups of landraces, largely on the basis of seed color, namely Arabi Abiad (white seed) and Arabi Aswad (black seed). Arabi Abiad is common in environments receiving between 250 and 400 mm annual rainfall; Arabi Aswad is cultivated in harsher environments with less than 250 mm annual rainfall. Although Vavilov had collected these two barley landraces by the beginning of the century, little is known about them. A few accessions have been included in the world collection, but as with many other crops no use has been made of these valuable genetic resources.

In the early 1980s, it was postulated that because barley landraces have been grown continuously since domestication without inputs in unfavorable and stress environments, their evaluation could teach a barley breeder a few lessons about adaptation to low-input, stress environments. It was also postulated that these lessons could prove useful to other breeders in countries where barley landraces are still predominant, as well as to breeders of crops mostly cultivated in stress environments (Ceccarelli 1984).

The objective of this chapter is to illustrate the use of landraces in the barley breeding program at the International Center for Agricultural Research in the Dry Areas (ICARDA), as an example of the contribution that landraces can make to increasing agricultural production, particularly for the rural poor in marginal environments. Implicitly, these arguments suggest that securing the continuity of the evolutionary processes within landrace polulations is of vital importance for future generations.

Collection and preliminary evaluation

In 1981, E. Weltzien made an extensive collection of barley in Syria and Jordan (Figure 3.2) from the fields of 70 farmers (60 in Syria and 10 in Jordan), who had been using their own seed for generations. One hundred spikes were collected at random from each farmer's field (Weltzien 1988). The spikes were kept separate, contrary to most conventional collection methods. This was a key factor in the subsequent utilization of the collection.

When the collected seed was multiplied off-season (planting in summer) as individual rows, each planted with the seed of one spike (head-rows), two main characteristics were noted. First, a high degree of seed dormancy was observed, with the material collected in southern Jordan showing a higher percentage of germination. Second, few of the rows were able to head and produce seed, with differences in the material collected at the same sites (Weltzien 1982). Additional information on the structure of the variation between and within collection sites was obtained when the material was evaluated under field conditions as individual rows (Weltzien 1988, 1989) or as plots (Weltzien and Fischbeck 1990). Significant genetic variation was found for seed color, growth habit, awn barbing, days to heading, culm length, leaf width, awn length, early growth vigor, lodging score, and powdery mildew resistance.

We recognize now that these were the first lessons the landraces were teaching, both by indicating traits of adaptive significance (such as vernalization requirement and seed dormancy) and by expressing the variability harbored within these populations. Three important findings, which were later confirmed, emerged from this preliminary evaluation. First, the genetic variability within the landraces was expressed in stress sites, where the heritability was even higher than in a non-stress site. Second, in a stress site the majority of landraces outyielded the check (improved) cultivars. Lastly, in the non-stress site the checks outyielded the landraces, though not always significantly.

From preliminary evaluation to breeding

Prior to 1984, the barley breeding program at ICARDA did not utilize landraces in a systematic fashion (Ceccarelli 1984), although the preliminary data were extremely promising, as indicated above. The procedure for utilizing the material of the barley landrace collection was first to assess the amount of genetic variation for agronomic and morphological characteristics, and then to determine the extent to which genetic diversity within the landraces was useful for breeding purposes. We focused attention primarily on Arabi Abiad and Arabi Aswad, the two barley landraces most widely grown in Syria.

In 1984, the barley breeding program began testing all of the breeding materials under typical growing conditions for barley in Northern Syria: strictly rainfed, predominantly in areas with low and erratic rainfall, and with little, if any, use of fertilizers, pesticides, or herbicides. The strategy was based on the assumption — later proven to be correct — that useful genetic variation for stress conditions could only be detected by testing breeding material under farmers growing conditions. To achieve this, we rented a farmer's field in an area that the breeding program had not previously used, referred to as Bouider, and we expanded the work already underway at Breda. Together with the experiment station at ICARDA headquarters in Tel Hadya, the experiment sites represent three distinct agricultural systems. Tel Hadya is a favorable high-input environment which lends itself to a wide choice of different crops. Bouider represents the opposite extreme: a typical low-input, high risk environment where barley is the only rainfed field crop. Breda is intermediate between the two, located at the beginning of the area where Arabi Aswad becomes the dominant landrace. The three sites are geographically close, located at 35 (Tel Hadya), 60 (Breda), and 80 km (Bouider) southeast of Aleppo, which provides an enormous advantage in terms of field operations. Table 3.1 shows the total rainfall at the three sites since the work on landraces began. Although rainfall does not convey all the information about climate — rainfall distribution and winter temperatures also play a determinant role — it is evident that there is a consistent rainfall gradient between the three sites, which makes the area unique in providing large climatic contrasts within short distances.

Table 3.1 Total Rainfall (mm) in the Three Experimental Sites Used by the Barley Breeding Program in Northern Syria

Year	Tel Hadya	Breda	Bouider
1984-1985	372.6	276.6	—
1985-1986	316.4	218.3	203.0
1986-1987	357.9	244.6	176.2
1987-1988	504.2	414.0	385.7
1988-1989	234.4	194.8	189.0
1989-1990	233.4	183.2	148.7
1990-1991	293.5	241.3	213.4
1991-1992	352.6	263.2	249.6
1992-1993	390.1	283.0	224.2
1993-1994	373.3	291.2	245.6
1994-1995	312.9	244.2	203.1
1995-1996	404.5	359.8	316.0
Long Term	328.9	267.8	235.2

In the season 1984-1985, 420 single-head progenies (lines) were evaluated at Breda in three trials. In the first two trials, we evaluated 280 lines representing 28 collection sites with 10 lines per collection site (Ceccarelli et al. 1987). Each trial contained 140 lines (10 for each of 14 collection sites) and four checks (Arabi Abiad and Arabi Aswad, and two improved cultivars

Harmal and Rihane-03). In the third trial, we evaluated 70 lines for each of two collection sites. Because the amount of seed was still a limiting factor, the lines were planted in two-row plots in the first two trials, and in four-row plots in the third trial. The following characters were measured or scored: growth habit, early growth vigor, cold damage, plant height, days to heading, days to maturity, grain filling duration, grain yield, spike length, peduncle extrusion, 1000 kernel weight, protein content, lysine content, and seed color.

Not surprisingly, a large and significant variability was found for virtually all of the characters measured. The mean squares between collection sites were nearly always significantly larger than the error mean square (Table 3.2). Also the variation within collection sites was almost always significantly larger than the error term. The "between collection site" component was in most cases significantly larger ($P < 0.01$) than the "within site" component.

Table 3.2 Mean Squares between and within Collection Sites for Agronomic Characters in Two Experiments with Single-Head Lines Derived from Local Cultivars

	Experiment 1			Experiment 2		
Character	Between Sites	Within Sites	Error	Between Sites	Within Sites	Error
Growth habit	6.97**	0.36**	0.2	5.05**	0.28**	0.2
Cold damage	8.08**	0.95**	0.49	9.36**	0.45	0.38
Days to heading	7.55**	4.86**	1.83	135.92**	8.90**	2.12
Days to maturity	8.96**	2.41 *	1.58	115.45**	2.87**	1.62
Grain filling	3.28**	2.66**	1.71	22.14**	6.91 **	2.29
Plant height	486.59**	43.44**	22.25	724.68**	36.06**	13.35
Spike length	0.83*	0.45*	0.3	5.78**	0.93**	0.4
Peduncle extrusion	64.20**	13.24**	3.15	141.43**	9.27**	3.42
1000 KW	168.88**	18.77**	4.8	270.06**	15.35**	5.22
% protein	1.26 **	0.71*	0.49	3.95**	0.66*	0.43
% lysine[a]	0.5	0.50**	0.29	0.92**	0.43**	0.25
Grain yield[b]	53.77**	4.87	4.59	67.13**	5.14**	3.25

* $P < 0.05$

**$P < 0.01$

[a] ($\times 10^{-3}$)

b ($\times 10^{3}$)

These data also quantified some of the key differences between the white-seeded and the black-seeded landraces (Table 3.3). These differences are of particular interest to plant breeders in verifying the firm belief of Syrian farmers that the black-seeded landrace is better adapted to dry areas and provides better feed for sheep than the white-seeded landrace. In this case, the use of lines with specific seed colors could become important to ensure quick adoption. Using the data of the third experiment we found that the black-seeded landrace is usually less vigorous in early growth, more cold tolerant and more productive under stress than white-seeded landrace. Arabi Aswad matures slightly earlier and has a shorter grain filling period than Arabi Abiad. Finally, plants tend to be taller, have smaller kernels, shorter coleoptile length, and shorter and fewer seminal roots. Some of these differences, such as those associated with phenology, cold tolerance, growth vigor, kernel size and plant height, are related to adaptation to dry and cold areas where the black type is predominantly cultivated. Syrian farmers often note the advantage of plant height under conditions of drought as one of the main reasons for preferring Arabi Aswad to Arabi Abiad in the drier areas. One of the primary effects of drought is a drastic reduction of plant height and a consequent reduction of straw yield. This increases the cost of harvesting, as it must be done by hand rather than by combine.

Table 3.3 Differences between the Black-Seeded (Arabi Aswad) and the White-Seeded (Arabi Abiad) Barley Landraces Commonly Grown in Syria

	Arabi Aswad (Black)		Arabi Abiad (White)	
Character	Mean ± s.e.	Range	Mean ± s.e.	Range
Growth vigor[a]	3.01 ± 0.09	4.48–1.35	3.69 ± 0.10	4.94–0.98
Cold damage[b]	2.10 ± 0.06	3.08–1.02	3.26 ± 0.08	4.68–1.58
Days to heading[c]	147.4 ± 0.22	153.0–141.5	147.7 ± 0.14	150.4–145.03
Days to maturity[c]	171.9 ± 0.30	177.6–168.8	173.8 ± 0.28	178.5–168.8
Grain fill. duration (days)	24.5 ± 0.26	30.5–19.50	26.1 ± 0.25	30.5–20.5
Plant height (cm)	52.1 ± 0.47	61.8–40.9	43.1 ± 0.46	53.4–33.4
Grain yield (kg/ha)	1769 ± 36	2480–944	1542 ± 40	2324–920
Protein content (%)	10.5 ± 0.05	11.6–9.7	10.6 ± 0.06	11.9–9.9
Lysine content (%)	0.43 ± 0.00	0.45–0.41	0.43 ± 0.00	0.46–0.40
1000 kernel weight (g)	35.7 ± 0.29	43.5–31.1	41.9 ± 0.35	47.9–34.6
Root number	57 ± 0.06	7.1–4.4	6.2 ± 0.05	7.4–5.0
Root length (mm)	55.8 ± 1.23	86.3–37.16	69.1 ± 1.11	99.3–43.3
Coleoptile length (mm)	47.5 ± 0.44	55.4–39.4	52.4 ± 0.55	61.4–41.4

[a] 1 = poor; 5 = good
[b] 1 = minimum; 5 = maximum
[c] Days from emergence

The most interesting aspect of this early work was the extraordinary amount of variability found *within* landraces as shown by the analysis of variance (Table 3.2) and the interval of variation (Table 3.3). The observation that landraces are composed of several genotypes is neither new nor original and has been reported for several crops, such as lentil (Erskine and Choudhary 1986), sorghum (Blum et al. 1991), bread and durum wheat (Porceddu and Scarascia Mugnozza 1984; Damania and Porceddu 1983; Spagnoletti-Zeuli et al. 1984; Damania et al. 1985; Lagudah et al. 1987; Blum et al. 1989; Elings and Nachit 1991), beans (Martin and Adams 1987a, 1987b), and both cultivated and wild barley (Brown 1978, 1979; Asfaw 1989).

In the case of Syrian barley landraces, the presence of such a high level of heterogeneity is not as obvious at first sight as it is, for example, in Ethiopian or Nepalese barley landraces. This hidden morphological variability might explain why Syrian farmers do not select within landraces either before or after harvesting but are able to distinguish between cultivars. Also, one could hypothesize that thousands of years of natural and human selection in a stress environment could have reduced the amount of heterogeneity through continuous selection for the most adapted genotypes. Not only does this not seem to be the case, but the variation available within the population appears to be large and of great value to a breeding program for stress environments and low-input conditions. This is most strongly indicated by the yield advantage of some of the pure lines extracted from landraces over both original landraces and some improved (modern) cultivars (Table 3.4).

Table 3.4 The Highest Yielding Pure Lines Extracted from Landraces in 1984-1985 in Breda (277 mm rainfall) Compared with the Two Commonly Grown Landraces (A. Abiad and A. Aswad) and Two Improved Cultivars (Rihane-0.3 and Harmal)

Entry	Seed Color	Plant Height (cm)	Grain Yield (kg/ha)
SLB 45-48	black	50.8	2480
SLB 39-31	white	42.4	2324
SLB 39-58	white	45.1	2287
SLB 45-83	black	55.9	2232
SLB 45-95	black	53.7	2227
SLB 45-40	black	61.5	2216
SLB 39-05	white	45.3	2189
SLB 45-04	black	55.2	2180
SLB 39-10	white	45.0	2162
SLB 45-90	black	61.8	2153
SLB 45-34	black	53.1	2146
SLB 45-76	black	53.6	2122
Checks			
A. Abiad (landrace)		45.4	1666
A. Aswad (landrace)		47.7	1547
Rihane-03 (modern)		49.4	1013
Harmal (modern)		45.9	1017
$LSD_{0.05}$		5.4	453

The data show a considerable yield advantage of the landraces over modern varieties in low rainfall conditions and with little or no use of inputs. These data have been confirmed in many comparisons between different types of germplasm in such an environment (Ceccarelli and Grando 1996) and, in part, explain the failure of introducing modern cultivars into the area. The most important information from a breeding point of view regards the amount of improvement which can be achieved by simply utilizing the variability present within landrace populations.

In addition to grain yield and other agronomic, morphological, and physiological characters, an unexpected amount of variability was found for disease resistance, particularly for yellow rust, powdery mildew, scald, and covered smut (Table 3.5) (van Leur et al. 1989). With the exception of covered smut, there was a significant variation both between and within collection sites. The response to diseases varied from absolutely or partially resistant types to highly susceptible lines. These findings challenge the common belief that landraces are disease susceptible, and therefore not worth the attention of modern plant breeders. The data (Table 3.5) indicate that although landraces appear disease susceptible because the majority of plants are susceptible, they do contain a small frequency of resistant individuals that are an important source of genes for disease resistance within an adapted genetic background.

Table 3.5 Mean Squares of Combined Analysis of Variance of Disease Readings on 140 Pure Lines Collected from 14 Collection Sites (10 lines per collection site) over 2 years

Source of Variation	df	Yellow Rust	Powdery Mildew	Scald	Covered Smut
Years	1	14781***	1215.40***	534.41 ***	2984.0***
Lines	139	1805***	10.92***	6.38***	47.1
Collection sites	13	7682***	63.28***	22.84**	133.7
Lines within co. sites	126	1199***	5.51**	4.68***	38.2
Lines × years	139	357**	4.1	2.48**	38.0***
Coll. sites × years	13	708***	9.40**	5.87***	108.1 ***
Lines w. sites × years	126	321*	3.56	2.13	30.7***
Residual	278	234	3.52	1.72	8.2

* $p < 0.05$
**$p < 0.01$
***$p < 0.001$

The presence of a high level of genetic diversity within populations — adapted to an environment where conventional breeding has failed — suggests that in addition to the need for continuous collection and both *ex situ* and *in situ* conservation, there is the almost unexplored possibility of using this large reservoir of genetic variation for plant improvement. To investigate further, we identified four strategies:

1. Develop highest yielding pure lines extracted from landraces into pure line varieties, after testing their stability in different environments (across sites and years);
2. Utilize pure lines extracted from landraces, which are superior for yield as well as for other characters including quality and resistance to insect pests and diseases, as parents in the crossing program to introduce additional desirable characters in an adapted genetic background;

3. Develop mixtures or multi-line varieties, constructed with a variable number of pure lines properly characterized for a set of agronomic characters. This permits us to exploit the buffering capacity of genetically heterogeneous populations in relation to stability and will conserve a certain amount of the evolutionary process within populations;
4. Evaluate lines with contrasting expressions of specific characters to quantify their adaptive role in stress environments, and use molecular techniques to identify, localize, and tag gene complexes or loci controlling quantitative traits (Quantitative Trait Loci or QTL) associated with adaptation.

The first three strategies aim to directly utilize the genetic variability within landraces, while the fourth aims to illustrate the usefulness of landraces as a unique source of information on mechanisms of adaptation to marginal environments, stress conditions, and low-input agriculture.

ICARDA initiated each of the four strategies within a few years of each other, with the exception of the molecular approach which began only recently. It was obvious from the beginning that these activities had two main objectives: to generate new cultivars for the dry areas of Syria; and to develop a methodology for landrace utilization which could be adopted with suitable modifications for other regions and crops where landraces are still available. To achieve the second objective, we designed the methods for exploiting the genetic variation between and within landraces with the expectation that they could be used by breeders in developing countries with limited resources. A key aspect of the methodology was to implement it with the same level of inputs used by farmers in resource limited environments. This would ensure that the products (pure lines and mixtures) would be beneficial to poor farmers and yield increases could be sustained.

Landraces as breeding material

Pure line selection: the short-term approach

Since 1985, we have systematically evaluated the collection of 7000 spikes described above, using a pure-line selection method to test between 300 and 400 lines each year under typical farmers' conditions. Farmers were invited to visit the plots and to make their own selection: their selection criteria (tall plants under drought and soft straw) were subsequently incorporated into breeders' criteria.

Twelve years after the initiation of the landrace breeding program, three quarters of the collection has been evaluated, three pure lines (two black-seeded lines, Tadmor and Zanbaka, and one white-seeded, named Arta — the only line officially released) are already growing in farmers' fields on an area of 500 to 2000 hectares each. Before 1981, Tadmor, Zanbaka, and Arta were three spikes among millions from the three collection sites, indicated in Figure 3.2 with the numbers 3 (central region), 42 (northeastern region), and 39 (southern region), respectively. Today, the progenies of those three spikes are growing in farmers' fields and out yield the local landraces by 10 to 25% without additional inputs.

Figure 3.2 Geographical distribution of the collection sites of the barley landraces in Syria and Jordan.

Figure 3.3 provides an example of the yield advantage which can be obtained in farmers fields with this strategy. Arta was compared with the local landrace (either Arabi Abiad or Arabi Aswad, depending on the location) in 69 farmers' fields in five provinces of Syria. The locations have been ranked in ascending order according to the yield of the local landrace. The superiority of Arta is larger at low yield levels than at higher yield levels: in the 23 lowest yielding locations, Ada always outyielded the local landrace — yields were similar in only one case — which suggests that Arta is especially beneficial to farmers in difficult environments. Arta was already showing its superiority when tested for the first time in the season 1984-1985 (SLB 39-58 in Table 3.4).

The evaluation of the landrace collection continues to generate new and useful lines every year. In 1994, for example, we evaluated all lines from four collection sites (Figure 3.2), one with white seed (site 24), and the other three with black seed (sites 21, 22, and 23). Even when improved lines, such as Arta and Zanbaka, are used as checks for grain yield and plant height, respectively, it is possible to find lines outyielding Arta by 36% in Breda and by 13% in Tel Hadya (Table 3.6). In terms of plant height it was possible to find lines significantly taller than Zanbaka in the three collection sites with black seed, and lines taller than Ada in the collection site with white seed.

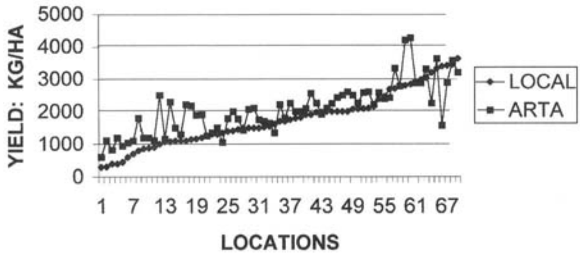

Figure 3.3 Grain yield of Arta compared with local barley in 69 farmers' fields in five provinces of Syria in 1996. Each cultivar was grown on plots of 1 ha.

Table 3.6 Variability between and within Four Collection Sites (see Figure 3.2) for Grain Yield in Two Locations, Days to Heading and Plant Height in 1994

Collection Site[a]	Breda (kg/ha)	Tel Hadya (kg/ha)	Heading	Plant Height (cm)
Site 21 (n = 86)				
means ± s.e.	1289 ± 24	2903 ± 34	111 ± 0.2	45 ± 0.4
min	891	2207	105	30
max	1837	3695	114	54
Site 22 (n = 79)				
means ± s.e.	1311 ± 21	2870 ± 26	111 ± 0.2	47 ± 0.5
min	706	2207	106	39
max	1754	3497	114	56
Site 23 (n = 70)				
means ± s.e.	1296 ± 23	2846 ± 51	110 ± 0.2	43 ± 0.6
min	832	1553	107	28
max	1837	3725	115	55
Site 24 (n = 64)				
means ± s.e.	1385 ± 25	3566 ± 54	110 ± 0.2	34 ± 0.6
min	884	1774	105	25
Max	1823	4491	113	50
Checks				
Arabi Abiad	1283	3489	105	36
Arabi Aswad	1108	2799	110	44
Arta	1352	3984	106	32
Zanbaka	1110	2744	109	50

[a] The number of lines evaluated (in parentheses).

The evaluation of the landrace collection has led to two primary successes. First, we have developed three varieties that have rapidly spread from farmer to farmer. Second, over the past 10 years we have identified, within the landraces, sources of resistance to most of the major barley diseases such as powdery mildew, scald, yellow rust, covered smut, barley stripe, and root rot, which have been selected for use as parental stocks (see next section). In some cases, such as the scald resistance of Tadmor, there is strong evidence that the resistance is not based on major genes and is therefore likely to be more durable.

The evaluation of pure lines described in this section is not a separate activity, but is conducted within the context of ICARDA's barley breeding program. Therefore, it has been possible during the years to make several comparisons between the landraces of Syria and Jordan and modern cultivars. In one such study (Table 3.7), 77 lines from Syrian landraces were compared with modern cultivars using the average grain yield of two stress sites (YS) and the average grain yield of three non-stress sites (YNS). The landraces have an average yield advantage of 60% under stress while the modern cultivars have an average yield advantage of 14%. In addition to the mean performance of the two types of germplasm, the interval of variation is very informative. All 77 lines from landraces yielded something under stress, while some of the modern cultivars failed; the best modern cultivars yielded almost as much as the best landraces. Under non-stress conditions, it was interesting to find that the yield of some landraces was not significantly inferior to that of the best modern cultivars.

Table 3.7 Grain Yield (kg/ha) under Stress (YS) and Grain Yield under Non-Stress (YNS) of Barley Landraces and Modern Cultivars in Syria

		YS[b]		YNS[c]	
Type of Germplasm	N[a]	Yield	Range	Yield	Range
Modern	155	488	0–893	3901	2310–4981
Landraces[d]	77	788	486–1076	3413	2398–4610
Best check		717		4147	

[a] Number of entries;

[b] Average of two stress sites;

[c] Average of three non-stress sites;

[d] Pure lines obtained by pure line selection within landraces.

The superiority of landraces does not depend on which improved germplasm is used in the comparison, or on the specific stress environment. For four breeding cycles, each containing different breeding lines, six-row genotypes unrelated to Syrian landraces were compared with two-row genotypes, which include both modern cultivars and Syrian landraces (Table 3.8). Under stress the two-row genotypes always yielded more than the six-row genotypes with a yield advantage ranging from 15 to 38%. This advantage is largely attributed to the landraces which, under stress, have a yield advantage of 28 to 54% over modern six-row types, and one to 35% over modern two-row types. When we compared the different types of germplasm for yield potential, the landraces are always the lowest yielding type of germplasm. In the dry areas of Syria, however, the probability of yields exceeding

3 tons per ha is about six times lower than the probability of yields less than 1.5 tons per ha (Ceccarelli 1996). Therefore, the lower yield potential of the lines extracted from landraces, specifically selected for stress conditions, is not a serious problem.

Table 3.8 Yield Potential and Yield under Stress of Six- (6) and Two-Row (2) Barley Genotypes; the Two Row are Classified as Improved (I) and Landraces (L) (Number of Genotypes in Brackets)

		Yield Potential		Yield under Stress	
Set[a]	Row Type	kg/ha[b]	6R = 100	kg/ha[c]	6R = 100
1989	6 (97)	5385 ± 64	100.0	561 ± 22	100.0
	2 (203)	5135 ± 56	95.3	644 ± 13	114.8
	2L (51)	4470 ± 87	83.0	759 ± 20	135.3
	2I (126)	5396 ± 67	100.2	608 ± 16	108.4
1990	6 (120)	3975 ± 83	100.0	458 ± 15	100.0
	2 (160)	3592 ± 81	90.4	632 ± 12	138.0
	2L (86)	43170 ± 87	79.8	705 ± 12	153.9
	2I (58)	4245 ± 138	106.8	521 ± 20	113.8
1991	6 (80)	4801 ± 68	100.0	754 ± 19	100.0
	2 (120)	4808 ± 50	100.2	955 ± 12	126.7
	2L (18)	4641 ± 154	96.7	966 ± 21	128.1
	2I (102)	4837 ± 52	100.8	952 ± 13	126.3
1992	6 (22)	4504 ± 82	100.0	440 ± 38	100.0
	2 (42)	4564 ± 89	101.3	575 ± 17	130.7
	2L (11)	4376 ± 72	97.2	661 ± 19	150.2
	2I (24)	4586 ± 46	101.8	558 ± 24	126.8

[a] Each set includes breeding lines and lines from landraces evaluated for 3 years. For each example the 1989 set contains lines evaluated in 1987, 1988, and 1989 in a number of locations.

[b] Average grain yield in those year-location combinations where the grain yield of all the breeding lines was one or more standard deviations higher than the average grain yield across all the year-location combinations of that set.

[c] Average grain yield in those year-location combinations where the grain yield of all the breeding lines was one or more standard deviations lower than the average grain yield across all the year-location combinations of that set.

One of the most important messages of the data shown in Tables 3.7 and 3.8 concerns the choice of the selection environment. It is dear from the two examples that, had the selection been done only under the high yielding conditions of a typically high input experiment station, the landraces would have had a short life as breeding material. As pointed out earlier, pure lines should be only one intermediate product in the overall strategy of using landraces in a breeding program. The value of some pure lines extracted from landraces underlines the importance of *in situ* conservation programs for maintaining those processes which can continuously produce new superior genotypes within landraces. The exploitation of the variability available within landraces is a simple and efficient way to improve the productivity of crops for which landraces are still available. Similar approaches to barley selection under low-input, stressed environments are currently underway in Ethiopia (Lakew et al. 1997), Tunisia, and Iraq. New collections of barley landraces have been made recently in Nepal and Eritrea to begin landrace improvement programs. Because of its potential for increasing crop production, however, using landraces as breeding material may lead to the replacement of landraces with improved pure lines, thereby endangering the evolutionary processes on which the success of the methodology is based.

Crosses: building on adaptation

Following from the identification of agronomically superior pure lines and sources of disease resistance within landraces, we initiated the second strategy to utilize pure lines as parental material in the breeding program. An example of the value of this approach is given in Table 3.9 where 514 breeding lines unrelated to landraces (improved) and 525 pure lines extracted from landraces are compared to lines derived from three types of crosses. The data were collected in a very dry site and year (Breda received 244 mm rainfall in 1995) where we measured grain yield, total biological yield, plant height, and harvest index, and in a relatively wet site (Tel Hadya with 313 mm rainfall) where we measured yield potential. As indicated earlier, the landraces yielded on average more than the improved lines under stress and had a lower average yield potential. Under stress, landraces and improved lines had a similar biological yield, but the landraces were, surprisingly, much shorter and had a higher harvest index — two characteristics usually associated with high yielding varieties when grown under optimum conditions.

Crosses between landraces and improved germplasm generated breeding material equal to land races in terms of grain yield and total biological yield under stress, and superior for plant height while maintaining a relatively high harvest index. Crosses between landraces and the wild progenitor of cultivated barley, *Hordeum spontaneum,* generated breeding material which is almost as good as that derived from crosses between landraces and improved germplasm. In this type of cross, the total biological yield and plant height are greater than in any other material, and both grain yield under stress and harvest index are probably underestimated because of the presence of some brittle-rachis genotypes. The last type of cross — improved × *Hordeum spontaneum* — generated the least promising type of breeding material, except perhaps for plant height.

Of the three types of crosses, crossing landraces with *H. spontaneum* has been the most promising avenue to improve plant height under drought: both plant height and straw softness are often indicated by farmers as the most desirable traits, particularly in dry areas. As mentioned earlier, a crop that remains tall even in dry years is important to farmers, because it reduces

Table 3.9 Grain Yield (kg/ha), Biological Yield (kg/ha), Plant Height (cm), and Harvest Index in Breda (1995) and Grain Yield in Tel Hadya 1995 (kg/ha) of Different Types of Breeding Material

Breeding Material	Grain Yield (BR95)[a]	Biological Yield (BR95)[a]	Grain Yield (TH95)	Plant Height (BR95)	Harvest Index (BR95)
Improved (n = 514)					
Mean	591 ± 8	1559 ± 17	4125 ± 27	23.2 ± 0.2	22.8 ± 0.3
Max	1201	4504	5812	40.3	41.3
Min	69	1559	1375	14.8	3.24
Improved ¥ Landraces (n = 214)					
Mean	775 ± 10	2678 ± 24	3883 ± 33	25.1 ± 0.3	29.1 ± 0.3
Max	1252	3658	5206	38	37.9
Min	259	1930	2630	16.9	11
Landraces (n = 525)					
Mean	752 ± 7	2549 ± 16	3657 ± 23	21.4 ± 0.1	29.8 ± 0.2
Max	1232	4027	5455	30.5	39.9
Min	320	1529	2250	13.1	16.5
Landraces ¥ *Hordeum spontaneum* (n = 133)					
Mean	724 ± 11	2829 ± 32	2797 ± 49	29.1 ± 0.4	25.9 ± 0.3
Max	1077	4007	4489	43.6	35.6
Min	369	2060	1515	20.5	11.5
Improved ¥ *Hordeum spontaneum* (n = 17)					
Mean	537 ± 37	2362 ± 111	2814 ± 118	27.1 ± 1.7	20.6 ± 1.2
Max	907	3681	3995	44.1	30
Min	306	1842	1780	19.2	11.4

[a] BR95 = Breda; TH95 = Tel Hadya 1995.

their dependence on costly hand harvesting, while soft straw is considered important in relation to palatability. Of 1532 lines tested at Breda in 1995, the mean plant height was 23.5 cm, the shortest lines were only 12.5 cm tall, and the most widely cultivated land race (Arabi Aswad) grew to a height of roughly 25 cm (Table 3.10). Some of the lines derived from crosses with H. *spontaneum* were taller than 40 cm. They were also significantly taller than Zanbaka, the pure line selected from Arabi Aswad (described earlier), which is already grown by some farmers for its plant height.

The characteristics of height and straw texture represent a drastic departure from the typical selection criteria used in breeding high-yielding cereal crops which favors short plants with stiff straw and high harvest index. Cultivars possessing the two characteristics considered important by farmers in dry areas would be unsuitable for high-yielding environments because of their lodging susceptibility, and would not be made available to farmers in

Table 3.10 Plant Height at Breda (244 mm rainfall) in 1995 of Barley Lines Derived from Crosses with H. *spontaneum,* Compared with the Barley Landrace Most Common in Dry Areas (Arabi Aswad) and with a Cultivar Selected Specifically for Plant Height under Drought (Zanbaka)

Cross / Name	Plant Height (cm)
H. spontaneum 20-4 / Arar 28 // WI2291/Bgs	43.5
SLB 45-40 / *H. spontaneum* 41-1	43.0
Zanbaka / *H. spontaneum* 41-2	42.5
Zanbaka / *H. spontaneum* 41-2	41.5
Mooc 9-75 / Arabi Aswad // *H. spontaneum* 41-3	41.0
Arabi Aswad	24.8
Zanbaka	26.0
Mean of all breeding lines	23.5
Maximum	43.5
Minimum	12.5
$LSD_{0.05}$	5.6

a traditional breeding program — a further indication of the importance of specific adaptation.

Eventually, an interesting pattern emerged in a number of experiments: not only under drought conditions did crosses with landraces largely out-yield crosses without landraces, but crosses with specific lines from land-races, such as Tadmor (Table 3.11), were superior to all other types of crosses. This might suggest the presence of blocks of genes in chromosomal regions with low frequency of recombination conferring a specific adaptation to stress environments — a hypothesis that will be tested with the techniques of molecular genetics.

Table 3.11 Yield under Drought Stress of Crosses with Tadmor and Crosses without Tadmor

Type of Cross	Grain Yield (kg/ha) under Stress
Crosses with Tadmor	1237
Crosses without Tadmor	604

The superiority of the crosses with landraces suggests that the strategy of using adapted germplasm in a breeding program is to capitalize on their specific adaptation to drought and low-input conditions rather than to consider them as sources of new useful genes as is the case in most plant breeding programs. Therefore, in breeding for stress environments, landraces should be regarded as recipients of few useful genes to be added to their adapted genetic background, rather than as donors of traits not available in "elite germplasm." This is conceptually similar to what breeders in favorable environments do: breeders find genotypes with high yield potential and good adaptation to high-yielding conditions and continue to build on them. The strategy is strengthened by the availability of genes for disease resistance within landraces. If a line extracted from landraces is agronomically superior but susceptible to a disease, the source of resistance is first sought among lines from the same collection site to preserve as much adaptation as possible, and secondly sought among lines from neighboring collection sites. Sources of disease resistance from germplasm adapted to different environments is the last resource. For these reasons, the best germplasm pool for the Fertile Crescent is now derived from crosses involving lines extracted from landraces.

Our assessment of the value of lines extracted from landraces as parental material in a conventional crossing program is based on those lines collected in 1981 and maintained *ex situ*. Lines with higher than average breeding value (defined as the value of an individual judged by the mean value of its progenies) are presumably being continuously produced by a combination of natural and human selection and by naturally occurring intercrossing. Thus, *in situ* conservation becomes essential to ensure that the flow of superior genetic material available within landraces into breeding programs is not a sporadic event, but a permanent component of the breeding process.

Mixtures: the long-term approach

Pure-line selection within landraces is potentially dangerous because it tends to replace genetically heterogeneous populations such as landraces with genetically pure lines. The adoption by Syrian farmers of three different pure lines almost at the same time and in a relatively small geographical area — some farmers even adopted two different lines at the same time — suggests that the danger may be less dramatic than the spreading of single genotypes over very large areas, as in the case of HYVs. There is also evidence that in marginal environments, replacement of landraces is often only partial (Brush 1995). In principle, however, genetic uniformity contrasts with the genetic diversity characteristic of the agricultural systems of poor farmers in marginal areas. In these systems, diversity is preserved at one or more levels by using different crops on the same farm, different cultivars of the same crop, and heterogeneous cultivars. Diversity reduces the risk of crop failures due to abiotic and biotic stresses, while monoculture of a single genotype maximizes such risk.

One wonders why millennia of natural selection operating in harsh environments on a crop such as barley in the Fertile Crescent have left us with heterogeneous populations rather than with a single or few genotypes with superior adaptation. Perhaps yet another lesson that landraces are teaching is that it is the *structure* of the population, in addition to the genetic constitution of the individual components, that harbors the secret of adaptation to difficult and unpredictable environments (see next section). Constructing mixtures with a number of superior, yet genetically different, pure lines selected from landraces is the long-term objective of using landraces in the barley breeding program at ICARDA. This would provide the added benefit of a population buffering mechanism to the adaptation of the individual components (Grando and McGee 1990; Lenné and Smithson 1994). Though perhaps more time-consuming and experimentally more complex than the first two strategies, developing lines with the view of constructing mixtures is an additional way of responding to the need of poor farmers for stable yields.

Therefore, over the last 10 years we have conducted trials with mixtures of variable numbers of superior, yet genetically different, pure lines selected from landraces to compare yield and stability of pure lines and landraces. The results have shown not only the superiority of some specific mixtures, but also that some pure lines have yield and stability levels similar to those of mixtures. In the most recent of these trials we compared mixtures and pure lines within the two barley landraces, Arabi Abiad and Arabi Aswad, in a range of environmental conditions including the typical low-input stressful environments of farmers' fields in dry areas. The mixtures were made with either black-seeded or white-seeded lines. The black-seeded group had mixtures of 72, 34, 17, and 5 lines, the white-seeded group had mixtures of 75, 34, 15, and 5 lines. The constituent lines were either unselected (the more complex mixture) or derived from one (mixtures with 34 lines), two (mixtures with 17 and 15 lines), or three (mixtures with 5 lines) cycles of selection. The material was evaluated from 1990-1991 to 1994-1995 in 22 environments with mean yields ranging from 614 to 4385 kg/ha.

Linear regression analysis showed that black-seeded material tends to have lower average grain yield, lower response to higher yielding conditions, and higher frequency of positive intercepts than white-seeded material. In both groups the mixtures with five selected lines had an advantage over the more complex mixtures with unselected lines. In the black-seeded group (Table 3.12), the mixture of five lines had both average grain yield and regression coefficient significantly higher than the landrace Arabi Aswad with a slightly larger intercept, but did not have a clear advantage over the individual lines. In particular the line SLB 5-96 had a high average yield (2164 kg/ha), combined with a relatively good response (b = 0.97) and a positive intercept (a = 99.9). In the white-seeded group (Table 3.13), the mixture of five components had an advantage over the landrace Arabi Abiad with a higher intercept, and had an advantage over the single lines, combining a high average grain yield (2263 kg/ha) with a good response (b = 1.05) and positive intercept (a = 32.9). The only other line with a positive intercept (SLB 9-98) had a very low average grain yield (1833 kg/ha) and low response (b = 0.79).

The results suggest that the two Syrian barley landraces possess different buffering mechanisms. In the white-seeded group, which is less adapted to stress conditions, the advantage of the mixtures was more evident than in the more stress-adapted black-seeded group. The advantage of both five-component mixtures over the more heterogeneous mixtures would indicate that yield stability may be achieved with a modest degree of heterogeneity,

Table 3.12 Average Grain Yield (kg/ha), Regression Coefficient (b), and Intercept (a) of Four Black-Seeded Mixtures, Five Lines, and Three Checks

Material	Grain Yield	b	a
Mixtures			
MIXB 72	2017	0.88	147.4
MIXB 34	2060	0.96	10.2
MIXB 17	2076	0.97	11.8
MIXB 5	2131	0.93	150.1
Pure lines			
SLB 5-96	2164	0.97	99.9
SLB 5-07	2179	0.98	97.6
SLB 5-86	1950	0.84	167.0
SLB 5-31	2266	1.05	35.7
SLB 5-30	1982	0.86	144.2
Checks			
Arabi Aswad	1896	0.83	116.7
Tadmor	1971	0.86	140.0
Zanbaka	1946	0.84	154.9
$LSD_{0.05}$	164		

Table 3.13 Average Grain Yield (kg/ha), Regression Coefficient (b), and Intercept (a) of Four White-Seeded Mixtures, Five Lines, and Three Checks

Material	Grain Yield	b	a
Mixtures			
MIXW 75	2237	1.15	-226.7
MIXW 34	2209	1.17	-277.1
MIXW 15	2174	1.08	-139.1
MIXW 5	2263	1.05	32.9
Pure lines			
SLB 9-63	2288	1.14	-144.4
SLB 9-71	2302	1.15	-152.3
SLB 9-76	2388	1.24	-248.5
SLB 9-09	2328	1.13	-86.8
SLB 9-98	1833	0.79	146.1
Checks			
Arabi Abiad	2202	1.14	-222.9
Arta	2414	1.19	-117.9
Harmal	2204	1.15	-248.8
$LSD_{0.05}$	164		

combined with the selection of superior lines. Like most studies on mixtures, these conclusions are strictly valid for the period under study. It may well be that the heterogeneity of the barley landraces from Syria has an advantage over longer periods of time than those usually covered by an experimental work. This is associated with the possibility, suggested by circumstantial evidence, of cross-pollination associated with an advantage of heterozygosity under drought (Einfeldt et al. 1996); this will determine continuous small adaptive changes in the genotypic composition of the landraces whose benefits can only be measured over longer periods of time than the 4 to 5 years of most experimental studies.

Understanding adaptation to stress

In addition to the contribution given to the breeding program, the landraces proved to be extremely useful experimental material for understanding adaptation to stress conditions in general, and the adaptive role of individual traits in particular. The genetic structure of landraces may be considered as an evolutionary approach to survival and performance under arid and semi-arid conditions (Schulze 1988). As indicated earlier, after millennia of cultivation under adverse conditions, natural and artificial selection have not been able to identify either an individual genotype possessing a key trait associated with superior performance or an individual genotype with a specific architecture of different traits. On the contrary, the combined effects of natural and artificial selection have led to an architecture of genotypes representing different combinations of traits. These populations can be extremely useful for understanding mechanisms that enhance stability in stress environments, not only from the population genetic point of view, but also for understanding the adaptive role of individual traits. In fact, although variable, landraces grown in environments characterized by a high frequency of stress conditions tend to present a high frequency of specific expressions of traits such as growth habit, cold tolerance, early growth vigor, and time to heading and maturity.

For example, barley lines extracted from landraces collected in five sites in the Syrian steppe (Table 3.14), compared with barley lines extracted from landraces collected in Jordan and with a wide range of modem barley genotypes, show a higher frequency of genotypes with prostrate or semi-prostrate growth habit, cold tolerance and short grain filling period, and a lower frequency of genotypes with good growth vigor and early heading. Their average grain yield in unfavorable conditions (Bouider 1989) was 984 kg/ha (ranging from 581 to 1394 kg/ha), more than twice the average grain yield of modem genotypes (483 kg/ha, ranging from crop failure to 1193 kg/ha). The average yield of the Syrian landraces in favorable conditions (3293 kg/ha) was 75% of the average yield of the modem germplasm in favorable conditions(4398 kg/ha). Although this particular set of data is based on one environment only, it confirms the existence of a trade-off between yield in

Table 3.14 Mean of Morphological and Developmental Traits[a] in 1041 Modern (Unrelated to Syrian or Jordanian Landraces) Barley Genotypes Compared with 322 Pure Lines Extracted from Syrian Landraces and 232 Pure Lines from Jordanian Landraces[b]

		Landraces	
Traits	Modern (n = 1041)	Syria (n = 322)	Jordan (n = 232)
1. Early growth vigor	2.5 b	3.2 a	2.4 b
2. Growth habit	2.8 c	4.0 a	3.1 b
3. Cold tolerance	3.0 a	1.3 c	2.3 b
4. Days to heading	117.9 b	121.2 a	116.9 c
5. Grain filling	39.3 a	35.5 c	37.4 b
6. YP	4398.0 a	3293.0 c	3947.0 b
7. YD	483.1 c	984.0 a	834.7 b

[a] Traits 1, 2, and 4-6 were scored or measured at Tel Hadya in 1987-1988 (504.2 mm rainfall), trait 3 was scored at Bouider in 1987-1988 (385.7 mm rainfall), and trait 7 was measured at Bouider in 1988-1989 (198 mm rainfall) on 521 modem lines, 92 Syrian landraces, and 86 Jordanian landraces. Means followed by the same letter are not significantly ($P < 0.05$) different based on *t*-test for samples of unequal size.

unfavorable conditions and yield in favorable conditions found in other sets of data based on a broader range of environments (Ceccarelli 1989).

Landraces collected in Jordan, from sites with milder winters than the Syrian steppe, have a higher frequency of genotypes with better early growth vigor, more erect habit, less cold tolerance, slightly longer grain filling period, and earlier heading than Syrian landraces. Their average grain yield in unfavorable conditions was only slightly lower (835 kg/ha) than Syrian landraces, while their average yield in favorable conditions (3947 kg/ha) was between that of the Syrian landraces and the modern germplasm. The highest yield of Syrian landraces under stress is not due to an escape mechanism, as they are the latest group in heading, and therefore could be a combination of resistance (or tolerance) and avoidance (prostrate habit and cold tolerance result in good ground cover) mechanisms.

Landraces are variable not only for above ground characteristics. A recent study (Table 3.15) shows that considerable variation exists for both the number and the length of seminal roots (Grando and Ceccarelli 1995) between different germplasm types. As mentioned earlier, seminal roots are important because in dry years they represent the only roots the plant produces. It appears that during the domestication of barley, the number of seminal roots has evolved from about three in H. *spontaneum* to five to seven in cultivated forms, while there has been a reduction in early root growth (root length) in modern varieties. In addition, the data show that for below ground characteristics — which are most likely important in relation to the use of water, one of the most limiting resources — there is

Table 3.15 Mean and Range of Variation for Number of Seminal Roots and Their Maximum Length at Zadoks Stage 10 in Three Groups of Barley Germplasm

	Number		Length	
Germplasm Group	Mean	Range	Mean	Range
Modern	5.5	4.6-6.1	96.5	70.8-115.3
Landraces	5.1	4.4-5.9	118.8	107.4-131.6
H. spontaneum	3.3	3.0-3.8	107.3	97.2-118.1
LSD	0.7[a]	0.4[b]	14.9	11.6

[a] $LSD_{0.05}$ for group means comparison.

[b] $LSD_{0.05}$ for entry means comparison.

considerable variability within landraces. Therefore, the advantages of heterogeneity discussed in the previous section may apply underground as well as above ground.

The comparison between breeding lines with the highest yield under stress and those with the lowest yield under stress (Ceccarelli et al. 1991) indicates that the former were significantly earlier, more cold tolerant, had better ground cover and larger kernels, were taller under drought, and yielded less in favorable conditions. However, the range of variation for each of these traits in the genotypes with the highest yield under stress always overlaps with the range of variation of the same trait in the genotypes with the lowest yield under stress. This shows that the final performance (grain yield in unfavorable conditions) can be achieved by several combinations of a number of traits, and the role of each individual trait depends on the frequency, timing, duration, and severity of stresses, and on the type of stress. Therefore, it is probably the interaction among traits which plays a key role in determining the differences in overall performance rather than the expression of any single trait in isolation. Therefore, efforts to associate the superiority of landraces under stress conditions with specific traits and transfer them into modern varieties is unlikely to be successful. Long-term and sustainable improvements of yield stability should be based on population buffering, using mixtures of genotypes representing different, but equally successful, combinations of traits, as occurs in landraces.

Conclusions

This chapter has demonstrated that the utilization of the genetic variability within a collection of landraces from Syria and Jordan in a barley breeding program for the dry areas of the Fertile Crescent has been a success. This success is associated with the variability within landrace populations sampled at a given moment in the evolutionary process — a variability which could not be captured in a gene bank. To successfully use landraces in crop breeding for difficult environments, it is important to understand the value of landrace breeding programs, as well as the areas of research which need further exploration.

The value of landraces in plant breeding programs

The importance of landraces (and of wild relatives) for present and future breeding programs can be appreciated only if some conventional concepts in plant breeding, such as the need for widely adapted cultivars and the need to select under optimum conditions, are challenged. Because of their evolutionary history, landraces are useful as breeding material in stress environments and for poor farmers, in areas where years of conventional plant breeding have had virtually no impact. Landraces have a long history of specific adaptation to low-input agriculture. Under low-input conditions, landraces have maintained a considerable amount of genetic variability. The adaptation of landraces to specific soil and climatic conditions therefore results in the development of a diversity of improved varieties. Therefore, the conservation and use of landraces can contribute to increasing agricultural production without requiring additional inputs, as well as the conservation of biodiversity within crops.

In breeding a crop for difficult environments and poor farmers, selection (not only testing) must be conducted within the target environment and under the agronomic conditions of the local farmers. Research stations can be utilized for seed multiplication. If most breeding continues to be conducted under the high-input conditions of the research stations, landraces will have a limited value and *ex situ* collections will continue to be poorly utilized.

There is, however, an implicit danger that a breeding approach based on the use of landraces may eventually accelerate the rate of genetic erosion. As indicated earlier, the success that is likely to occur by exploiting the variability within landraces through pure-line selection may lead to the widespread adoption of the pure lines and the disappearance of the landraces. One approach to prevent the replacement of landraces is that of participatory plant breeding. In implementing a participatory plant breeding program where farmers select from a wide range of germplasm present in their own fields, we have found that farmers select material derived from landraces more frequently than other material. Farmers also want to know the nature and origin of the material they select, particularly that which is performing well. Their understanding that the landraces they have grown over long periods of time are capable of continuously generating new types which can improve the living standards of present and future generations could become a key factor in promoting their interest in conserving the original landrace, while adopting new lines and mixtures. Therefore, participatory plant breeding could generate considerable farmer interest in *in situ* conservation.

Research areas for further exploration

Although successful, the work on landraces described in this chapter leaves a number of questions unanswered. For example, we still ignore the complexity of the population structure of landraces both in terms of the number of different homozygotes (since barley is a self-pollinated crop) and the occurrence and frequency of heterozygotes due to natural cross-pollination. Similarly, we do not know if there is any geneflow between H. *spontaneum* and cultivated barley. If geneflow does occur, how frequent is it, and what role does this introgression play in the performance and stability of the landraces?

We have no systematic description of the nature and amount of genetic variability available in landraces in different geographical areas, of the spectrum of adaptation of populations collected in different areas, and of the frequency of useful traits. Yet, such information is essential to define the areas of adaptation of different landraces (which would be useful where germplasm is lost in specific areas due to natural or political calamities), and to identify priority areas for *in situ* conservation.

One research area that requires major emphasis is that of mixtures. In some crops (including barley), the release of mixtures as cultivars can be done even in the presence of the restrictive regulations on variety release and seed certification, because virtually all seed comes from the informal seed system. By evaluating bulk samples with farmers' participation, successful bulks can find their way directly into the informal seed system. For other crops, years of breeding for uniformity have generated the widespread aversion of breeders to heterogeneity, which contrasts dramatically with the heterogeneity of the material best adapted to difficult environments. The type of mixtures that should be investigated depends on the context in which the crop is grown. In the case of barley in the Fertile Crescent, for example, it might be necessary to consider the presence of H. *spontaneum* if it can be shown that there is indeed geneflow between wild and cultivated barley.

Landraces are adapted to their environment, and they fit into the farming systems of their area of adaptation. They are often essential components in the diet, and in many cases they are the only food or feed available. The welfare of people depending on landraces should and can be improved not by replacing landraces but by improving them. Maintaining the genes of landraces in breeding programs and through *in situ* conservation programs is a moral obligation toward those many farmers who have maintained landraces over millennia.

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