

GENOTYPE BY ENVIRONMENT INTERACTION AND INTERNATIONAL BREEDING PROGRAMS

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Abstract

The paper addresses the issue of genotype by environment (G x E) interaction in relation to the distribution of germplasm from international to national breeding programs. Theoretical aspects of G x E interaction and of selection versus testing environment are reviewed. The importance of specific adaptation to maximize yield and yield stability in stress conditions is highlighted in barley and lentil. We conclude that repeated cycles of selection at a few sites have a high probability of reducing the frequency of genotypes specifically adapted to environmental and/or agronomic conditions not represented at those sites. Therefore, a wider and earlier devolution of the selection work done by International Agricultural Research Centers (IARCs) to breeders of national programs will increase the chances of exploiting positive G x E interactions. It will also address the needs of small, resource-poor, subsistence farmers and reduce the danger of narrowing genetic diversity within crops and regions. This is an efficient way of making breeding programs in less developed countries more self-reliant which is a major objective of International Research Centers.

Introduction

International nurseries and training are major contact points between national and international breeding programs. The nurseries are distributed to national programs on request and are tested in a wide range of conditions. In self-pollinated crops the level of heterozygosity varies between the nurseries, but most are fixed or nearly fixed lines. For example, the frequency of segregating populations in the nurseries distributed by the Cereal Improvement Program at ICARDA in the last five years ranged from 20 to 30%. The fixed or nearly fixed lines in the other nurseries were included on the basis of 5-6 years of selection in a limited number of environments.

There are three ways in which the environment and selection strategy determines the characteristics of lines eventually reaching national programs:

First, selection is often conducted in favorable environments (Hildebrand, 1990, Simmonds, 1991) as it is believed that these allow the full expression of genetic differences for yield potential. But, with the exception of disease and lodging resistance, genetic differences under ideal conditions may be irrelevant because such conditions have little in common with farmers' fields.

Second, the initial selection environments represent only a small sub-set of the range of environments in which the lines will be tested by national breeding programs. Even when some initial selection environments are stress environments, it is unlikely they cover all stresses experienced in the test environments. Thus genotype x environment (G x E) interactions are bound to reduce selection efficiency.

Third, high mean yield over a set of environments is a common selection criterion. High average yield is frequently associated with high yield in good environments. These lines will go to national breeding at the expense of those specifically adapted to poor environments (Yau, 1991; Stroup et al., 1992).

National scientists have been trained on these principles and evaluate international nurseries in conditions similar to those used by international programs with a high probability of identifying high yielding lines suitable for good conditions. At the adoption level, farmers who use similar, good conditions (defined as "progressive" farmers) benefit from new varieties but those who do not continue with landraces and benefit little from the breeding done by International Centers (Bramel-Cox et al., 1991; Simmonds and Talbot, 1992).

This paper discusses the theoretical background to selection in environments which differ from the target environment, and suggests a different approach to the relationship between national and international breeding programs, using the ICARDA barley and lentil projects as examples.

Theoretical considerations

From a theoretical standpoint, germplasm distribution through international nurseries is a product of the relationship between selection and testing environments (Rosielle and Hamblin, 1981; Ceccarelli, 1989; Simmonds, 1991). In general terms and with reference to yield, this is a case of indirect selection where the breeder aims to improve a primary character by selecting for a secondary character. The justification for indirect selection is a higher heritability of the secondary character but as pointed out by Falconer (1981), measures of the same character in two different environments should be regarded as two different characters.

With specific reference to selection in stress and non stress environments, Rosielle and Hamblin (1981) showed that selection for tolerance to stress will reduce yields in non stress environments and also reduce the average yield in stress and non stress environments. Recently Simmonds (1991), using numerical simulation concluded that selection for low yielding environments must be conducted in low yielding environments; that using selection environments with intermediate yield levels is ineffective; and that alternating selection cycles in low and high yielding environments (shuttle breeding), is also ineffective. Similarly Smith et al. (1990) concluded that selection in low input conditions is essential if significant yield gains for such conditions are to be achieved. Experimental evidence indicates that the choice of selection environments affects the response of genotypes to changing environments (Hildebrand, 1990; Ceccarelli and Grando, 1991a).

The efficiency of indirect versus direct selection can be predicted from the heritability and the genetic correlation coefficient:

$$CR^X/R^X = r^G h^Y / h^X$$

where CR^X is the correlated response in environment X when selection is done in environment Y, R^X is the direct response when selection is done in environment X, r^G is the genetic correlation coefficient between A^X and A^Y (A is an hypothetical trait), h^Y and h^X are the square roots of heritabilities of A in the two environments (Falconer, 1981).

When $h^Y = h^X$, the maximum value of CR^X/R^X is 1 when $r^G = 1$. Therefore, when heritabilities are the same, direct selection will always be more effective because the genetic correlation coefficient will always be less than one. The argument commonly used in favor of selecting in good environments is that heritabilities are higher in favorable than in poor environments (Blum, 1988). However, with low genetic correlation coefficients (0.1 - 0.2), h^Y must be at least 5 to 10 times higher than h^X for CR^X to be greater than R^X (Table 1). Heritability alone is not sufficient to determine the optimum selection environment. Moreover, when r^G is negative the magnitudes of h^Y and h^X are irrelevant. Estimates of r^G , h^Y and h^X clarify when selection in non-stress environments is effective for genotypes that will have to grow in stress environments. This is a problem of strategic importance to breeders in both national and international programs.

Materials and Methods

Barley and lentil are two autogamous crops domesticated in the Fertile Crescent. In lowland Mediterranean environments lentil is usually grown between 300 and 400 mm annual rainfall while barley occurs between 200 and 500 mm isohyets. Above 400 mm the predominant food legume is the more profitable and water-demanding kabuli chickpea, while barley still competes with wheat. Below 300 mm lentil cultivation is limited by its water requirement and barley remains the only possible crop while agriculture is possible.

The data on barley were obtained from sets of barley yield trials conducted between 1986 and 1992. The number of entries varied between 180 lines (1990-92) and 332 lines (1986-88). Experimental design, plot size, and agronomic management have been reported in detail elsewhere (Ceccarelli & Grando, 1991a, 1991b). The lines represent a wide range of genetic material with regard to earliness, row type and adaptation. The data used here were obtained from three locations in northern Syria (Tel Hadya, Breda and Boudier with long-term average rainfall of 332, 274 and 201 mm, respectively), one location in Lebanon (Terbol, long-term average rainfall of

485 mm) and one location in Cyprus (Athalassa, long-term average rainfall of 321 mm). Estimates of genetic correlation coefficients were obtained from sites differing in mean yields as described by Ceccarelli et al. (1992).

Results

We compared the performance of barley genotypes in the lowest and highest yielding test sites for the last eight cropping seasons. The average yield of all lines and the yield of the best 5% of the lines selected at low and high yielding sites, respectively, were recorded with total rainfall at the lowest and highest yielding sites (Table 2). The average yield at the high yielding sites was almost four times that of the low yielding sites.

The lines selected as high yielding in good conditions yielded similarly to the population mean at the low yielding sites and, on average, 39% less than lines selected for high yield in stress conditions. At the high yielding sites the situation was reversed; lines which yielded highly in stress conditions yielded similarly to the population mean and yielded on average 24% less than high yielding lines selected in non stress environments. These results were independent of flowering date and early leaf area growth (Hamblin, 1992).

The data indicate that, at a phenotypic level, correlated selection differentials in low yielding conditions for selections made in high yielding conditions are either negative or low. However, such differentials are only useful in predicting correlated responses to selection if the genetic correlation coefficient is known (Falconer, 1981). Estimates of genetic correlation coefficients between grain yield measured in low and high yielding sites were therefore obtained from 58 pairs of yield trials in four cropping seasons (Ceccarelli et al., 1992). Among the 58 estimates of r_G , 27 were negative (Table 3) and only 8 of the 31 positive values were greater than 0.4, six of those being associated with low average yields at the highest yielding sites (ranging between 1812 and 3180 kg/ha). When the genetic correlation coefficients are related to the yield levels of the two environments used, high grain yield in high-yielding conditions and high grain yield in low-yielding conditions appear to be under the control of different sets of alleles at most (or several) loci. The few estimates of genetic correlation coefficients available in the literature (Atlin & Frey, 1989, 1990; Ud-Din et al., 1992) are in agreement with those reported here.

The barley data suggest that when lines are tested across a wide range of environments, a cross-over G x E interaction (Fig. 1) is common (Ceccarelli, 1989; Ceccarelli and Grando, 1991a). This has also been found in a number of other crops (Simmonds, 1981, 1984; Hildebrand, 1984; Blum, 1988 pg. 25; Lawn, 1988; Smith et al., 1990; Ud-Din et al., 1992).

In contrast to barley, the performance of lentil is relatively more homogeneous within its narrower production zone of 300-400 mm around the Mediterranean basin. The evidence for this is circumstantial in that several lentil cultivars have been released by national programs as a result of the exploitation of the region's landraces. Selections from Jordanian landraces are registered in Iraq, Jordan, Lebanon and Syria and are in pre-release multiplication in Libya; Lebanese germplasm has been released in S.E. Turkey, and a selection from a Syrian landraces has been released in Algeria and Tunisia (ICARDA, 1993).

However, a more specific adaptation emerges around the Mediterranean Sea in moisture regimes outside this relatively narrow production zone. Under low rainfall conditions (<300 mm annual rain) high yield is associated with drought escape through early flowering (Silim et al., 1993), and high yield under irrigation is associated with specific adaptation to irrigated conditions (Hamdi et al., 1992).

At higher elevations in West Asia (>800 m elevation), lentil is of necessity spring-sown because lentil landraces do not survive the severe winter cold although winter-sown winterhardy cultivars can yield 50-100% more than the traditional spring sown crop (Sakar et al., 1988).

When lentil was introduced into the Indo-Gangetic plain around 2000 BC (Cubero, 1981) it was exposed to environmental conditions very different from those at its origin. A reconstruction of the phenological problems associated with the initial spread of the crop into the Indo-Gangetic plain was inadvertently made when lentil selections were introduced there through early ICARDA

international nurseries. Lentils selected in West Asia, when sown in India and Pakistan, mostly came into flower when the indigenous lentils were maturing (Table 4) (ICARDA, 1982, 1983, 1984). It is now known that temperature and photoperiod control time to flower in lentil and that Indian germplasm is both more sensitive to temperature and less sensitive to photoperiod than germplasm from West Asia (Summerfield et al., 1985, Erskine et al., 1990).

Figure 1, based on Ceccarelli and Grando (1991a) and extracted from numerous published results obtained with the joint regression analysis (Finlay and Wilkinson, 1963), illustrates the large G x E interactions shown by barley and lentil. The actual point where the cross-over occurs varies with the crop and environment. In barley, for example, it occurs between 2 and 3 t/ha. The actual value indicates the boundary between environmental domains that may require different breeding strategies.

Implications for International and National Breeding Programs

International breeding programs aim to assist national programs to increase agricultural production by developing superior cultivars. The interaction between these programs has been largely a one-way, "top-down" process (Simmonds and Talbot, 1992) where international programs develop germplasm and national programs test and eventually release it as varieties. This has often excluded the use of locally adapted germplasm and encouraged its displacement. It has also discouraged the use of mixtures which might cope with high variability in both biotic and abiotic stresses (Ceccarelli, 1984; Grando and McGee, 1990; Ceccarelli et al., 1991).

International breeding programs must adopt a positive interpretation of genotype by environment interaction (Stroup et al., 1992) if they are to address the need of small, resource-poor, subsistence farmers, who have been by-passed by the Green Revolution. This involves devolution of selection to national programs and selection conducted in conditions as similar as possible to those of the farmers.

The first step is to replace fixed or semi-fixed lines with less advanced genetic material or segregating populations. Early distribution of breeding material reduces the danger of useful lines being discarded because of their relatively poor performance at some test sites. This problem is illustrated by the 288 six-row barley lines evaluated both in the Magreb countries (Libya, Tunisia, Algeria, Morocco) and in ICARDA's preliminary yield trials grown at three sites in Syria (Tel Hadya, Breda and Bouider) in 1991/92. In the Magreb countries visual selection was used, whereas at ICARDA selection was for yield potential, yield under stress, and heading date. 103 entries were selected at ICARDA and 154 in the Magreb but only 49 of these were selected at both ICARDA and the Magreb suggesting a high probability of discarding lines potentially useful in other areas.

To exploit specific adaptation fully and make positive use of G x E interactions, ICARDA and its national partners are replacing gradually the traditional international nurseries with earlier generation material. When fully implemented, national programs in a given geographical area (e.g. north Africa) will receive from ICARDA's barley breeding program only targeted F² segregating populations and yield trials consisting of lines derived from these F²'s selected in-country. Selection between F² populations will be in the different agroecological environments within each country under conditions as similar to farmers' fields as possible. Lines selected from superior F² populations will be advanced at ICARDA with minimal selection and then yield tested in different locations within each country. In the future F²'s for the Magreb region will be derived from crosses between parents identified by national breeding programs on the basis of specific adaptation to the environments and needs of their countries. Further details are given in Table 5.

Similar principles are applied in the ICARDA lentil breeding program but on a wider geographical scale. While no attempt is being made to breed for the specific adaptational requirements within the current production zone of lowland Mediterranean environments, specific programs are underway for high elevation areas and the Indo-Gangetic plain. Because cross-pollination in lentil is more difficult than in barley, it is difficult to produce sufficient seed of F² populations for distribution. ICARDA's relative advantage in crossing and in rapid generation advancement through growing the F¹ generation in a high elevation summer nursery are exploited.

Targeted bulk segregating populations are then distributed to specific national programs in the F⁴ generation for single plant selection in the target environment by national programs. Progeny rows and simultaneous yield and disease testing follow. As the result of this joint effort, 75% of test entries in the National Uniform Variety Trial in Pakistan in 1990 were selected by the national program from ICARDA-supplied segregating populations. The best of these lentil selections are now in on-farm trials and being placed in the crossing block for making jointly agreed crosses for the next cycle.

Conclusion

An understanding of the adaptation of the crop is basic to its effective improvement by plant breeding through both national and international programs. The extent of G x E interaction within the target area has determined the need for specific as opposed to general adaptation in two crops in contrasting ways. Both crops are adapted to low-rainfall, highly variable environments. In such variable environments there is a considerable need for specific adaptation. At ICARDA the response to the specific genotype by environment interactions of each crop has been to develop individual targeted breeding programs using early generation material for specific regions.

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LEGEND OF FIGURES

Figure 1. Yield (t ha^{-1}) in environments of increasing yield potential of typical barley genotypes selected (A) for high yielding environments and (B) for low yielding environments.

Table 1. Values of CRX/RX as functions of the genetic correlation coefficient (r_g) and the ratio between the square roots of heritabilities in high (h_Y) and low yielding (h_X) environment (modified from Ceccarelli et al., 1992).

r_g	h_Y/h_X									
	1	2	3	4	5	6	7	8	9	10
0.1	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.2	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
0.3	0.3	0.6	0.9	1.2	1.5	1.8	2.1	2.4	2.7	3.0
0.4	0.4	0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6	4.0
0.5	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0
0.6	0.6	1.2	1.8	2.4	3.0	3.6	4.2	4.8	5.4	6.0
0.7	0.7	1.4	2.1	2.8	3.5	4.2	4.9	5.6	6.3	7.0
0.8	0.8	1.6	2.4	3.2	4.0	4.8	5.6	6.4	7.2	8.0
0.9	0.9	1.8	2.7	3.2	4.5	5.4	6.3	7.2	8.1	9.0
1.0	1.0	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0

Table 2. Overall mean yields and mean yields of 5% highest yielding lines of barley (kg ha⁻¹) selected under high and low yielding conditions, with rainfall (mm) at each site.

LOW YIELDING SITES	RAIN	YIELD			
		MEAN	SELECTED AT LOW YIELDING SITES	SELECTED AT HIGH YIELDING SITES	
1985	BR	178	743.17	1284.59	779.79
1986	BO	180	1138.34	1935.26	1340.79
1987	BR	164	673.9	1019.19	654.66
1988	BO	382	2910.38	4199.48	3383.132
1989	BO	184	687.16	1287.18	658.52
1990	BR	183	471.10	794.17	429.46
1991	BO	207	1050.22	1693.24	953.110
1992	BO	223	902.18	1305.26	1030.46
Means			1072	1690	1153
HIGH YIELDING SITES					
1985	TH	373	3489.29	3339.114	4210.49
1986	TH	316	4007.35	4139.78	4970.70
1987	TH	343	2668.23	2739.113	3613.35
1988	TH	499	4420.45	4672.173	6100.67
1989	AT	214	5824.60	4874.315	7814.107
1990	TR	317	3346.26	3066.118	4122.27
1991	TR	559	4740.54	4705.253	6073.65
1992	AT	321	4627.45	4799.171	5793.99
Means			4140	4042	5337

^a

BR = Breda, BO = Bouider, TH = Tel Hadya (BR, BO and TH are in Syria) AT = Athalassa (Cyprus), TR = Terbol (Lebanon)

Table 3. Range of genetic correlation coefficients between yield of barley measured at a low yielding and at a high yielding site, and ratio between correlated and direct response to selection (CR/R) from a total of 58 trials conducted in four cropping seasons. (modified from Ceccarelli et al., 1992).

Year	negative	0-.2	.2-.4	.4-.6	.6-.8	.8-1.0	CR/R > 1
1986-87	6	1	4	2	2	2	1
1988-89	13	2					0
1989-90	5	7	2				0
1990-91	3	4	2	2		1	0
Total	27	14	8	4	2	2	1

Table 4. Time to flower (days) of lentil germplasm accessions from India and Syria at two locations of similar latitudes but contrasting mean photoperiod and temperature prior to flowering (extract from ICARDA, 1983).

	Terbol, Lebanon	Islamabad, Pakistan
Latitude (°N)	34	33
Photoperiod (h)	12.2	10.9
Temperature (°C)	6.6	12.5
Accessions:		
ILL 4380 (India)	130	114
ILL 4400 (Syria)	133	132

Table 5. Barley breeding for specific adaptation.

YEAR	MAJOR ACTIVITIES
1 (winter)	Crosses (mostly 6 row x 6 row)
2 (winter)	F ¹ grown at Tel Hadya (ICARDA's headquarters). Distribution of F ² populations (12 sets)
3 (winter)	F ² 's are grown as two-rows plots in 12 locations and in a spaced planted plot at Tel Hadya under optimum growing conditions. Selection between F ² populations at the 12 sites and individual plant selection within selected F ² 's at Tel Hadya
4 (winter)	Seed increase of F ³ families at Tel Hadya under optimum growing conditions Evaluation of F ³ bulks (of selected F ² 's) and elimination of F ³ families from poor F ³ bulks
5 (winter)	Initial yield trials with F ⁴ families at 12 locations (unreplicated) Seed increase at Tel Hadya of F ² -derived F ⁴
6 (winter)	Preliminary yield trials (F ⁵) at 20 locations (2 reps) Seed increase of F ² -derived F ⁵
7 (winter)	Advanced yield trials (F ⁶) in 20 locations (4 reps)
8 (winter)	Best lines (F ⁷) enter national testing systems