Agronomic performance of crosses between Nordic and exotic barleys

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Summary

Exotic germplasm may be useful for the improvement of agronomic performance of barley breeding material. This study was conducted in order 1) to evaluate if it is possible to improve performance of Nordic barley breeding material by utilizing exotic germplasm sources (unadapted landraces and *H. spontaneum*), 2) to evaluate incorporation of exotic germplasm into a genetic base widely adapted to the agro-ecological conditions of the extreme Scandinavian north as well as to the base adapted to the conditions of the south of this geographical region, and 3) to evaluate whether an index composed of several traits corresponded to 'breeder's phenotypic evaluation' of the progenies. Earliness, straw length, number of ears/plant, yield/plant, seed shattering, persistence of awns and an index computed from these traits were studied in Swedish and Finnish 4-way crosses along with their adapted parents. Most of the crosses headed earlier than their adapted parents and none of the crosses with only cultivated barleys as parents. Transgressive segregates were also found in progenies with *H. spontaneum* parents. Incorporation of exotic barleys was most successful into the local genetic base. Comparisons between indices and breeder's phenotypic evaluation suggested reconsideration of evaluation methods early in parent development.

Introduction

Exotic germplasm has been mainly used as a source of single genes in breeding programmes (for review see Carver and Taliaferro, 1992; Kalloo, 1992). However, in long-term 'base broadening programmes' where the aim is to widen genetic variation of locally adapted breeding populations (Simmonds, 1993), the stress is put on the improvement of a wide spectra of economically important traits. This development of segregating populations produces a much wider variation than generated by adapted \times adapted crosses. For barley, which is discussed in this paper, the possibility of obtaining novel variation from landraces and from its wild progenitor *Hordeum vulgare* L. ssp. *spontaneum* is great due to a large diversity of adaptive characters found in these sources and the ready intercrossabili-

ty of cultivated and wild barleys (Frankel and Soulé, 1981; Nevo, 1992).

Initially, performance suffers when exotic germplasm is introduced into elite genepools due to the disruption of 'coadapted gene complexes' or introduction of inferior alleles. Therefore, exotic germplasm has been used in the improvement of primary economic traits only to a limited extent. However, in long-term breeding it may be useful to break-up 'gene complexes' and by intermating exotic and adapted germplasms maximize the potential for new valuable recombinants (Kenworthy, 1980; Kannenberg and Falk, 1991). It is also unlikely that germplasm currently used in crop improvement contains all the desirable genes which control a particular quantitatively inherited trait (Gerloff and Smith, 1988). In addition, ever-increasing performance gaps between elite and exotic material

would make the use of exotics decreasingly attractive if long-term pre-breeding efforts are neglected (Smith and Duvick, 1989).

One important problem in the utilization of genes controlling 'metric characters' is that they are not necessarily expressed in the exotic parents. For example, studies on wild sorghum (Bramel-Cox and Cox, 1988), oat and barley (Frey et al., 1984) show a negative relationships in performance between wild parent and progeny. Therefore, it is suggested that the value of exotics should be measured when incorporated in the locally adapted genetic base (Bramel-Cox and Cox, 1988; Simmonds, 1993; Veteläinen, 1994a). This approach may demand large scale investment, extensive recombination and several generations to achieve progress, but simultaneously it provides an opportunity to widen variation in the local genetic base. It can be even worthwhile at the same time to establish a new local population that is independent of the local breeding material but good enough to provide desirable parents for future breeding (Simmonds, 1993).

In this investigation we analysed a sample of F_2 progenies from two experimental breeding populations. Each of the progeny had both adapted and exotic parents. The objectives of the study were: (a) to evaluate if it is possible to improve agronomic performance of Nordic, locally adapted barley material by utilizing various exotic germplasm sources, (b) to evaluate incorporation of exotic germplasm into a genetic base widely adapted to the agro-ecological conditions of the extreme Scandinavian north as well as to the base adapted to the conditions of the south of this geographical region and (c) to evaluate whether an index composed of several traits corresponded to a breeder's phenotypic evaluation of the progenies.

Material and methods

Plant material

The ten crosses (Table 1) used in the study were selected from two experimental barley genepools designed for southern Sweden and southern Finland earlier described by Veteläinen (1994b). A number of plants was taken at random from each F_1 population to produce the F_2 generation for field experiments. All of the crosses had two parents adapted to their respective geographical area and in addition, two exotic parents, with the exception of two which had only one exotic parent. The exotic parents were either unadapted landraces from China and Pakistan or wild barley, *Hordeum vulgare* L. ssp. *spontaneum* (hereafter called *H. spontaneum*) lines from Jordan and Syria. More detailed information of the exotic material can be found in Veteläinen (1994a). The crosses were selected from both of the genepools so that one pair of Finnish (Fi) and Swedish (Sw) crosses had the same exotic parents (Table 1). The amount of exotic germplasm in the crosses varied from 25% to 50%. The crossing scheme (Table 1) was established as follows: (parent 1 × parent 2) × (parent 3 × parent 4). Wide parental diversity was the second selection criterion for the crosses of the experiment.

Field experiment

The experiment was conducted at two locations, and the first was sown on peat and the second on clay soil at Boreal Plant Breeding in Jokioinen, Finland during summer of 1994. The growing season was extremely warm and dry. The seeds were space planted with two replications in each location. Each plot consisted of six rows with 20 cm between rows and 10-15 cm between plants within the row. Two rows of a cross and one of each adapted parent was sown in a plot. The flanks were border rows to provide competitive balance for side rows. Plots were randomized within a replication. Fertilizer application per ha was 80 kg N at the peat site and 110 kg N at the clay site. All plots were weeded. The ears of plants selected for measurements from crosses with a H. spontaneum parent were bagged after anthesis to collect the shattered seed.

Traits

In each location and replication, 50 random F_2 plants of each cross and 15 plants of each adapted parent were measured. Seven traits were recorded from each plant (Table 2). Earliness was recorded as the number of days from planting to the date when the first head emerged. Straw length (cm) was measured from the highest tiller of the plant. Number of ears per plant was counted late in the growing season. Heading synchrony was recorded in 5 different classes (Table 2), but in the final statistical analyses the classes 3.1 and 3.2 were merged. Yield was measured in grams. Seed shattering was checked on head samples before threshing. Persistence of awns after threshing was recorded in 3 classes. An index was constructed separately for 2- and 6-rowed plants as follows:

Table 1. Crosses, their origin and parental lines (L = unadapted landrace, S = Hordeum vulgare ssp. spontaneum line)

Cross no	Origin of the cross	Parent 1 (adapted)	Parent 2	Parent 3 (adapted)	Parent 4
Fi 1	Finland	Jo 1621	H 4241 (L)	Hja 80138	H 7614 (L)
Fi 2	Finland	Kalle	H 4248 (L)	Meltan	H 7405 (L)
Fi 3	Finland	Kinnan	H 4035 (L)	Pohto	H 3064 (S)
Fi 4	Finland	Hja 83054	Ob 264	Mette	H 3042 (S)
Fi 5	Finland	Arttu	H 4175 (L)	Jo 1545	H 4246 (L)
Sw 1	Sweden	Alfa	H 4241 (L)	Aisling	H 7614 (L)
Sw 2	Sweden	Korinna	H 4248 (L)	Sv 892052	H 7405 (L)
Sw 3	Sweden	Golf	H 4035 (L)	Jet	H 3064 (S)
Sw 4	Sweden	Nancy	Sv 89412	Sv 898219	H 3042 (S)
Sw 5	Sweden	Ida	H 4175 (L)	Milka	H 4246 (L)

 $\begin{aligned} \text{INDEX} &= \mathbf{i}_{ear.em} + \mathbf{i}_{straw} + \mathbf{i}_{no/ears} + \mathbf{i}_{synchrony} + \\ \mathbf{i}_{yield} + \mathbf{i}_{shattering} + \mathbf{i}_{persistence} \end{aligned}$

Results

Environmental variation

For index computation, each trait was divided into two to four classes (Table 2). The scale for 2-row plants was from 7 to 23 and for 6-row plants from 7 to 24. In addition, breeder's phenotypic evaluation of the progeny was carried out at the peat location in order to study whether evaluation corresponded to the index used. In breeder's evaluation plants were classed as 1) discarded, 2) acceptable, 3) good or 4) very good. The differences in performance were expected to be most pronounced at the peat site.

Statistical analyses

The General Linear Models (GLM) procedure of the Statistical Analyses System (SAS Inst., 1990) was used for the analyses of variance, which were carried out separately for parents and crosses. The data from parents was used as control of environmental variation. REG procedure was used for regression analysis, where cross means were dependent variables and parent means regressors. Tukey's test was used to compare the means of a cross with both of its adapted parents and means between crosses. Spearman rank correlation (Sokal and Rohlf, 1981) was used to calculate the relationship between index and breeder's evaluation. Transgression for each cross was computed against its better adapted parent mean over both experimental sites.

The results from analysis of variance are shown in Table 3. The location was a significant source of variation for all the traits measured, except for number of ears per plants within crosses. The four metric traits measured exhibited greatest mean values at the peat site (data not shown). Replications within locations were tested only for parents and they were not significantly different for ear emergence, straw length and yield per plant.

Metric traits

Generally, the mean values (data not shown) for crosses were at least at the same level as some of the adapted parents. However, none of the means of the crosses was significantly better than the best parent, although some of the crosses were slightly earlier than the best parent. The Finnish crosses with H. spontaneum parents (Fi 3, Fi 4) had lower mean yields than both of the adapted parents. Yet, this pattern was not so very clear in Swedish crosses with the same H. spontaneum parents. Finnish parents were somewhat earlier (with general mean 62,9 days) and had fewer ears per plant than Swedish parents (64,2 days). These differences were also found in crosses (61,7 and 63,8 days, respectively). Finnish parents had somewhat higher yields per plant in this experiment. Yield comparisons between crosses (data from Tukey's test not shown), showed that the pairs with the same exotic parents were similar, except in one case (Fi 4, Sw 4). As expected, the coefficients

Trait	Phenotypic class	Score for index
Ear emergence, days	1) < 60	4
	2) 61- 70	3
	3) 71- 80	2
	$4) \ge 81$	1
Straw length, cm	1) 15- 36	1
	2) 37– 54	2
	3) 55- 85	3
	4) 86–100	1
Number of ears/plant	1) ≤ 3	1
2-row	2) 4- 8	3
	3) 9– 13	2
	$4) \ge 14$	1
Number of ears/plant	1) ≤ 2	2
6-row	2) 3- 6	4
	3) 7- 10	3
	$4) \ge 10$	1
Heading synchrony	1) All the ears/plant emerge and ripen	4
	almost simultaneously	
	2) Heading continues longer than in	3
	class 1, but almost all the ears ripen	
	3.1) Heading continues for a long	1
	time and all the ears do not ripen	
	3.2) Heading continues indefinitely	1
	4) Uniculm type	2
Yield, g/plant	1) 0- 7	1
	2) 8-14	2
	3) 15-20	3
	4) 21- 27	4
Seed shattering	1) Non-brittle spike	2
	2) Brittle spike	1
Persistence of awns in	1) Non-persistent	3
threshing	2) Partly persistent	2
	3) Persistent	1

Table 2. Phenotypic classes and score values for index computation

of variation (data not shown) were generally larger for the crosses than for the parents.

Percentages of plants in each cross with earliness, yield/plant and index above the best parent mean are given in Table 4. When both of the adapted parents in the cross were of the 2-row type, the percentage for the 6-row plants was not counted. This was the case when only exotic parents were of 6-row type. The percentage of transgressive segregates for earliness ranged from 14 to 75%, while the range for yield was from 9 to 32%. Crosses with *H. spontaneum* parents had the highest percentages of transgressive segregates for earliness for earliness for earliness percentages.

and lowest for yield in Finnish crosses. This pattern was not as evident in the Swedish crosses.

Relationships between parents and cross means are presented in Figure 1 as scatter plots from regression analysis. Regression was significant for all four traits at the 95% level. From 39 to 54% of variation of metric traits in crosses could be explained by the mean of adapted parents.

Traits indicating wild state

Crosses including *H. spontaneum* as a parent segregated for three undesirable traits: seed shattering (11%),

Table 3. Significance of main effects and interactions for four traits

Source of variation	df	Ear emergence	Straw length	No ears/plant	Yield/plant
Parents					
- Fi vs. Sw	1	**	NS	**	**
- lines/varieties	19	**	**	**	**
- locations	1	**	**	**	**
- reps. within locations	2	NS	NS	*	NS
- lines \times locations	19	**	**	*	**
Crosses					
- Fi vs. Sw	1	**	**	**	NS
- between crosses	9	**	**	**	**
- locations	1	**	**	NS	**
- crosses \times locations	9	**	**	**	**

*, ** significant at the 5% and 1% level, respectively.

Table 4. Percentages of plants from each cross with earliness, yield/plant and index above the best adapted parent mean

Cross	Earliness	Yield/plant	Index	
			2-row	6-row
Fi 1	49	20	_	27
Fi 2	53	22	58	11
Fi 3	75	9	38	8
Fi 4	63	12	10	-
Fi 5	28	22	27	13
Sw 1	70	32	50	-
Sw 2	31	22	24	-
Sw 3	71	21	36	-
Sw 4	14	31	11	-
Sw 5	49	31	45	-

persistence of awns (56%) and late unsynchronous tillering habit (11%). Late unsynchronous tillering was even found in crosses with only cultivated exotic parents, ranging from 5 to 10% in each cross.

Index

To acquire an overall estimate of agronomic performance for each plant individual, an index was formed. Frequency distributions for indices are presented in Figures 2 and 3. Indices for 2-row plants varied from 12 to 21 (Figure 2) and for 6-row plants from 14 to 22 (Figure 3), i.e. none of the plants had a 'perfect' combination of traits. The crosses with *H. spontaneum* parents (Sw 3, Sw 4, Fi 3 and Fi 4) had the least favorable frequency distributions both in 2- and 6-row

Table 5. Spearman correlation coefficients between index (7 = composed from seven traits, 4 = from four traits and 3 = three traits) and breeder's evaluation

Trait	Index	2-row	6-row
Breeder's	7	0.44**	0.55**
evaluation	4	0.26**	0.23**
	3	0.21**	0.12*

*, ** significant at 5% and 1% level respectively.

material. On the average, the Swedish crosses had a higher frequency of 2-row plants with high indices whereas the Finnish ones had a higher frequency of 6-row material with high index. Generally, crosses had a higher frequency of plants with low indices than the parents (frequency distribution not shown).

When considering positive transgressive segregation for the index (Table 4), a similar pattern was found between Finnish and Swedish crosses with *H. spontaneum* parents. Crosses Fi 4 and Sw 4 had the lowest percentages of transgressive segregates in their progeny, while Fi 3 and Sw 3 had a relatively high frequency of superior segregates among their progeny. It is also notable that crosses Fi 4 and Sw 4 had three adapted parents in their pedigree while the other crosses had only two.

Correlation analysis (Table 5) was carried out to study the association between the index and breeder's evaluation of the crosses (Figure 4). Analysis was made using an index constructed from seven (all the traits measured), four (ear emergence, straw length,





Figure 1. The relationship between the means of adapted parents and crosses (a) ear emergence, (b) straw length, (c) number of ears per plant and (d) yield per plant.

number ears/plant and heading synchrony) or three (ear emergence, straw length, number ears/plant) traits. The correlation was highest when all the seven traits were included in the index. When traits expressing the wild state were omitted from the index, the correlation between index and breeder's evaluation was reduced.

Discussion

In this study agronomic performance was analyzed using four metric traits. In addition, an index combined from these traits and three traits indicating a level of wild state was used as a measure. Most of the crosses headed earlier than their adapted parents and the highest percentage of transgressive segregates was 75%. However, long-day conditions at the experimental site may have been a stress factor for exotic germplasm and thus, caused early 'forced' heading in their progeny. Therefore, in cases where early heading was followed by late development and maturity, earliness may not be considered as expression of adaptedness. As a consequence one should evaluate exotic \times adapted progenies using extensive information of plant development from heading to maturity in order to obtain better understanding of earliness.





Figure 2. Frequency distributions of index in 2-row progenies.

None of the crosses outyielded the adapted parents, but transgressive segregates for yield were found in each of the crosses. Nevertheless, one should consider the yields measured on individual plants with some caution. In order to obtain more comprehensive information on yielding capacity, further testing with normal seeding rate under conditions of competition is needed. Yet, data from mean yields may give some indication of which type of exotic germplasm is most useful for yield improvement. The crosses with a *H. spontaneum* parent, had with one exception, the lowest yields, while crosses with only cultivated exotic parents



Figure 3. Frequency distributions of index in 6-row progenies.



Figure 4. Breeder's evaluation of crosses at the peat location. Classes 1 = discarded, 2 = acceptable, 3 = good and 4 = very good.

yielded somewhat better. Therefore, if fast progress is desired, utilization of cultivated exotic parents may be the right strategy. When using wild germplasm, such traits as persistence of awns after threshing increases the number of selection cycles needed to achieve acceptable yield quality.

Observed transgression and relatively low parentprogeny regression suggests that evaluation of the exotic \times adapted progenies may give a better estimate of the potential of the germplasm source than evaluation of the parents *per se*. Similar evidence for barley yields has been obtained earlier by Rodgers (1982). Examples of this are the crosses Fi 3 and Sw 3 which produced extremely early progenies, while this was not the case for the second pair of crosses with *H. spontaneum* parent. Both *H. spontaneum* accessions used as parents in this study were recently evaluated by Veteläinen (1994a) and found to be significantly later than the adapted parents. Thus, evaluation for earliness of the

Breeder's evaluation

progeny seemed to be a more useful strategy than evaluation of the parents *per se*.

In order to gain a general impression of agronomic performance, several traits have to be considered simultaneously. This is important, particularly when evaluating progenies with exotic parents which carry 'wild' and undesirable traits. The most favorable frequency distributions for the index were found in the crosses with only cultivated barley as parents. Similar judgements were made by the breeder (Figure 4). Still, positive transgressive segregates were found in progenies with H. spontaneum parents. This is in agreement with earlier studies (Vega and Frey, 1980; Rodgers, 1982; Frey et al., 1984; Veteläinen, 1994a), which showed that wild barley may be used as a source when improving agronomic performance. However, the differences between crosses with different types of exotic sources (wild vs. cultivated) gives an indication for parent selection. Crosses with wild parents bring undesirable traits such as a late unsynchronous tillering habit, which is a negative trait in areas with a short growing season (Dofing and Knight, 1992). Crosses with only landraces may be used more readily in short-term breeding activities. However, in the long run, wild accessions may be a valuable for increasing genetic variation.

An interesting question in incorporation and utilization of exotic material is whether to recombine it with a narrowly adapted, high-yielding or possibly generally adapted, high-yielding base. In our study, Finnish material was well-adapted to northern marginal conditions with a short growing season, while material from Sweden represented a more widely adapted southern Scandinavian base. This division was done using mainly earliness as a criterion since a short growing season is the outstanding risk factor to yield in Finland (Mukula and Rantanen, 1986). Unfortunately, the growing season 1994 was extremely warm and thus the differences in heading dates were insignificant. However, differences in mean ear emergence between Finnish and Swedish parents and crosses indicated the importance of a local genetic base. Regression analysis showed that only 39% of the variation in ear emergence in crosses could be explained by the adapted parents. Thus the effect of exotic germplasm is of considerable importance to adaptation. Yet in this case, none of the exotic sources seemed to have negative effects on heading dates, although information of maturity would have been needed for proper evaluation of earliness. The Finnish crosses and especially crosses with a wild parent had fewer transgressive segregates for yield than Swedish crosses. This may indicate that a narrowly adapted, perhaps genetically more fine-tuned, base is more sensitive to the incorporation of exotic germplasm than a widely adapted base with more frequent gene-flow from various sources in its breeding history.

The last aspect of this study was to compare how differently composed indices corresponded to breeder's phenotypic evaluation of the progenies. Correlation increased with increasing number of traits included in the index. Still, it was only moderate. There may be two explanations for this condition that should be considered when evaluating new breeding material. Firstly, all plants were evaluated as either 2- or 6-row types. Morphologically peculiar and degenerate segregates were not recorded. However, this was presumably recorded by the breeder and hence lowered the correlation. Secondly, a breeder probably avoids more or less consciously to select plants of 'odd phenotype'. This may be one of the reasons for low correlation and consequently, may hinder new plant types from entering active breeding populations. Thus, if a breeder aims at conserving genetic diversity in a breeding programme, he may have to reconsider his evaluation methods in the early phase of parent development. Finally, the low number of classes of the breeder's evaluation has probably also lowered the numerical value of the correlation coefficient used.

Our study indicates that utilization of exotic germplasm is valuable in improvement of agronomic performance. It is especially important, when there is a need to increase genetic diversity in the breeding material. Furthermore, this study supports the idea that the value of exotics should be measured for agronomic performance when incorporated in the locally adapted genetic base. In the long run the most useful strategy is probably to establish new, independent breeding populations for parent development.

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