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Regression analysis of yield stability is strongly affected by companion test varieties and locations – examples from a study of Nordic barley lines

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Abstract The suitability of regression analysis for studying the phenotypic stability of grain yield was investigated using a collection of 220 Nordic barley lines. Linear regression explained 26–52% of the genotype × environment (GE) interactions in different groupings of the material. The regression coefficient, b_i, measures the yield response of the *i*-th genotype to improved environmental conditions. Deviations from regression, S^2_{di}, have been used to estimate Tai's stability parameter, λ_i, which is a measure of the phenotypic yield stability in the agronomic sense. Repeatability of b_i, λ_i, and grain yield was studied by means of correlations between estimates obtained in each experimental year. Yield had the highest repeatability, with correlations between years ranging from 0.57 to 0.85. In this study, regression coefficients and λ_i-values were not repeatable, i.e. genotypes reacted differentially to the yearly climatic variations. Six-rowed (6r) barleys had higher responsiveness, but lower mean yields, than two-rowed (2r) barleys. This is partly due to the history of selection of 6r-barleys, which mainly originate from regions with low potential yield levels, i.e. Finland and Norway. In general, responsiveness and stability were not correlated with yield. The highest-yielding lines had $b_i \approx 1$. The response pattern of the different types of barleys used in this study show that responsiveness can be changed by recombination.

Key words Adaptation · Barley · Genotype × environment interaction · Regression analysis · Repeatability

Introduction

The relative magnitude of the genotypic variance expressed in different environments is crop specific (Allen et al. 1978). Some plants perform well in a wide range of different environments, while others express their genetic potential better in a specific environment. Within a relatively homogeneous climatic region there may be different agro-ecosystems, reflecting variations in soil type, crop rotation, and degrees of cropping intensity (Austin 1988). In order to obtain accurate estimates of yield, growth response and the stability of individual cultivars, it is essential that both a large range of environmental indices, and a uniform distribution of environments over the range, are included in studies of genotype × environment interactions (Eberhart and Russell 1966; Skrφppa 1984).

The most widely used selection criteria for high and stable performance are mean yield, regression response on site mean yield (b_i), and deviations from regression (S^2_{di}) (Yates and Cochran 1938; Finlay and Wilkinson 1963; Eberhart and Russell 1966; Langer et al. 1979; Becker and Léon 1988). Mean grain yield of all genotypes at each location may be interpreted as an environmental index. According to the 'agronomic' concept of phenotypic yield stability, only deviations of a genotype from these environmental indices are considered as cases of instability (Becker 1981). In regression analysis, cultivars with $b_i = 1$ and zero deviations from regression are said to be agronomically stable. Pfeiffer and Braun (1989) stated that the yield of a good genotype in the environment with the poorest growth conditions sould exceed or equal the average of all entries. Lin and Binns (1991) combined three procedures for selecting stable cultivars: (1) regression analysis and cluster analysis to sort the data by similarity of mean yields and b_i's, (2) a superiority measure for assessing a cultivar's performance relative to a location maximum, and (3) stability analysis to assess variation over years.

The selection of new varieties in high-yielding environments is a more or less unconscious selection of varieties with a high regression coefficient relative to other candidates (Shabana et al. 1980; Reysack et al. 1993). Positive correlations between mean yields and regression coefficients are therefore frequently reported

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(Perkins and Jinks 1968a; Knight 1970; Langer et al. 1979; Becker 1983; Pfeiffer and Braun 1989). However, there is also empirical evidence that there is no close relationship between yield and regression coefficient (Becker 1981; Pham and Kang 1988). Any relation will depend upon the test environment and the history of selection (Ceccarelli and Grando 1991), and may be species specific (Yue et al. 1990). The repeatability of the regression coefficient seems to be good in some cases (Léon and Becker 1988; Simmonds 1991; Nissilä 1992; Jalaluddin and Harrison 1993).

The aims of the present investigation have been to analyze the suitability of using regression analysis to explain genotype × environment (GE) interactions of Nordic barley cultivars, and to estimate the repeatability and correlations between grain yield, responsiveness and the yield stability of Nordic 6r- and 2r-barleys.

Materials and methods

Plant material

The barley materials used in this study were mainly inbred lines and pure-line varieties. A detailed description of origin, pedigrees etc. can be found in Nurminiemi et al. (1996). Some of the entries were heterogeneous populations of nearly homozygous individuals, such as bulks, multilines of landraces. The 220 lines and cultivars were further divided into five subsets on the basis of earliness or row type. Subset EARLY consisted of 37 six-rowed (6r) and three two-rowed (2r) early maturing feed barleys. Subset 6R included all 71 6r-barleys, while subset 2R comprised 149 2r-barleys. Late-maturing cultivars made up subset LATE, which comprised 146 2r and 34 6r feed and/or malting barleys. Subset ALL included all 220 genotypes.

Description of experimental locations

Experiments were conducted at the following locations: Hφjbakkegård (55°40′N 12°18′E) is the experimental farm of the Royal Veterinary and Agricultural University, Denmark; Korpa (63°46′N 20°15′W) is an experimental field of the Agricultural Research Institute, Reykjavik, in southern Iceland; Röbäcksdalen (63°51′N 20°16′E) is an experimental farm of Svalöf Weibull AB, near Umeå, in northern Sweden, Svalöv (55°57′N 13°8′E) is the main experimental farm of Svalöf Weibull AB in southern Sweden; Viikki (60°15′N 25°3′E) is the experimental farm of Helsinki University in southern Finland, and Ås (59°40′N 10°48′E), is the experimental farm of the Department of Biotechnological Sciences at the Agricultural University of Norway in South-East Norway.

Temperature is the most important climatic factor restricting plant growth in the north of Scandinavia, while drought is most limiting in the southern regions and areas east of the Scandinavian mountain chain (SNP 1992). Rainfall and heat sums for the growth seasons have been recorded from the nearest climate record stations, and compared to long-term mean values (Table 1).

The known pattern of macro-climatic factors makes part of the variation in weather conditions more predictable than the yearly fluctuations in temperature, radiation and rainfall (Allard and Bradshaw 1964; Knight 1970; Lin and Binns 1988; Pfeiffer and Braun 1989). Predictable parts of the variation in weather conditions, together with variations in edaphic, biotic and management factors, create genotype × location (GL) interactions. Unpredictable climatic factors contribute to GY- and GLY-interactions.

Experimental design

The experimental design was a special type of incomplete blocks with two complete replications at each location (Aastveit 1977). The material was divided into series A and B (which correspond to subsets EARLY and LATE, respectively). Within each series the accessions were randomly grouped into blocks of 20 lines. Accessions were randomized within blocks, and blocks were randomized within replication in every year. All blocks contained two reference varieties 'Arra' (6r) and 'Ida' (2r). Plot size varied from 5 m^2 to 10 m^2, depending on location, and the sowing rate was 440 seeds/m^2.

Statistical analysis

The model for the conventional analysis of variance of the combined data expresses the observed mean yield as:

$$Y_{ijk} = \mu + G_i + E_j + Bl_{jk} + (GE)_{ij} + e_{ijk},$$

$(i = 1, 2, \ldots m, j = 1, 2, \ldots n, k = 1, 2, \ldots r)$, where μ is the general mean; G_i and E_j represent the effect of the i-th genotype and j-th environment, while $(GE)_{ij}$ stands for the genotype-environment interactions, Bl_{jk} for the block effect of the k-th replication at the j-th environment, while e_{ijk} designates the random errors associated with the k-th replication of the i-th genotype at the j-th environment. Regression analysis was performed according to the Eberhart and Russell (1966) model:

$$Y_{ij} = \mu_i + b_i I_j + \sigma_{ij},$$

where μ_i is the mean of the i-th genotype over all environments, I_j the environmental index ($I_j = \bar{Y}_j - \bar{Y}$, location mean − grand mean), b_i the linear regression coefficient of the i-th genotype, and σ_{ij} the deviation from regression. The coefficient of regression is estimated as:

$$b_i = \textstyle\sum_j Y_{ij} {*} I_j / \sum_j I_j^2,$$

and the deviation mean squares as:

$$S_{di}^2 = \textstyle\sum_j \sigma_{ij}^2/(n-2)\,(= \mathrm{MS}_{\mathrm{residual}}).$$

Regression can be tested by an approximate F-test: $F = [\sum_j \sigma_{ij}^2/(n-2)]/\mathrm{MS}_e$, where MS_e is the pooled experimental error mean square. If an approximate F-test, $\mathrm{MS}_{\mathrm{regression}}$: $\mathrm{MS}_{\mathrm{residual}}$, is significant, then genotypes have different responses. In this study, Tai's (1971) lambda-value,

$$\lambda_i = [\textstyle\sum_j \sigma_{ij}^2/(n-2)] \times r/\mathrm{MS}_e,$$

(r = no. of replications) was used to estimate the yield stability of genotypes. If $\lambda_i = 1$, then the squared deviations from regression, σ_{ij}^2, are much smaller than the error mean square, and the linear component explains the GE-interaction. The hypothesis that $b_i = 1$ is tested by a t-test:

$$t = (b_i - 1)/\mathrm{SE}(b_i),$$

where the standard error of b_i is the square root of the deviation mean squares divided by the sum of squares of environmental indices:

$$\mathrm{SE}(b_i) = \sqrt{\mathrm{MS}_{\mathrm{residual}}/\textstyle\sum_j I_j^2},$$

and the t-values follow the Student's t-distribution with $n-2$ degrees of freedom. Also the difference between a pair of genotypes can be tested: $t = b_i - b_{i'}/\mathrm{SE}(b_i - b_{i'})$, where the standard error of the two regression coefficients $(i \neq i')$ is estimated as: SE $(b_i - b_{i'}) = \sqrt{[(\mathrm{SE}\,b_i)^2 + (\mathrm{SE}\,b_{i'})^2]}$. In this case t-values follow the Student's t-distribution with $2{*}(n-2)\,df$. Grain yield and b_i's were normally

Table 1 Length of growth season is measured as days from sowing to harvest. Cumulative rainfalls and cumulative heat sums (> + 5°C) were recorded from 1 week before sowing date, and from the date of sowing, respectively, until harvest. The relative values presented in parenthesis are based on long-term averages

Location	Year	Date of sowing	Daylength at sowing (h)[g]	Length of growth season, (days)	Rainfall in mm () = % of normal	Heat sum > 5°C () = % of normal
Højbakkegård[a]	87	11.5	14	141	408(147)	1095(84)
	88	18.4	14	119	175(80)	1110(115)
	89	10.4	14	126	212(94)	1046(109)
Korpa[b]	88	16.5	19	133	420(117)	596(93)
	89	22.5	19	140	550(136)	555(87)
Röbäcksdalen[c,d]	88	25.5	19	128	456(173)	1058(104)
	89	29.5	19	126	202(78)	982(97)
Svalöv[d]	87	28.4	14	140	358(115)	1198(93)
	88	20.4	14	117	232(93)	1200(119)
	89	10.4	14	128	227(86)	1133(111)
Viikki[e]	87	23.5	16	129	375(213)	893(78)
	88	11.5	16	91	145(147)	1029(118)
	89	7.5	16	113	208(162)	1230(116)
Ås[f]	87	7.5	16	131	428(127)	927(78)
	88	10.5	16	98	287(118)	1068(115)
	89	9.5	16	112	275(97)	1015(94)

Meteorological data have been obtained from the following sources:

[a] Dept. of Agricultural Sciencies, Section of Soil and Water and Plant Nutrition, The Royal Veterinary and Agricultural University, Copenhagen, Denmark

[b] Agricultural Research Institute, Keldnaholt, Reykjavik, Iceland

[c] Swedish Meteorological and Hydrological Institute, Stockholm, Sweden

[d] Svalöf Weibull AB, Svalöv, Sweden

[e] Finnish Meteorological Institute, Helsinki, Finland

[f] Meteorological data for Ås, Dept. of Physics, Agricultural University of Norway, Ås

[g] Nilsen (1983); SNP (1992)

distributed, while the probability of normal distribution for λ_i-values varied from 0.67 to 0.88. The repeatability of b_i, λ_i and grain yield was studied using Pearson correlation coefficients between estimates obtained in different years.

Results

Average grain yields

Average grain yields in kg/ha are shown in Table 2. The cool and rainy growth season of 1987 caused lower mean yields in this year than in 1988 and 1989, especially at Højbakkegård (Tables 1 and 2). Korpa and Röbäcksdalen always had the lowest mean yields in subset EARLY due to shorter growing periods than at the southern locations.

At Højbakkegård and Svalöv it is usually possible to sow 3–4 weeks earlier than at Ås and Viikki. This gave remarkably higher mean yields for 2r-lines and later maturing materials (subsets 2R, LATE and ALL, Table 2) at Svalöv in 1988 and 1989. Denmark and Scania comprise a relatively uniform growth area (SNP 1986), and one would therefore expect the mean yields at Højbakkegård to be most similar to those at Svalöv. Pre-summer drought caused low mean yields at Ås in 1989 and at Viikki in 1988 (especially in subsets EARLY and 6R). The adaptation of 2r- and 6r-lines to the diverse climate of the Nordic countries have been discussed by Nurminiemi et al. (1996).

Genotype × environment interactions

Estimated GE-interactions were highly significant ($P < 0.001$) in subsets 6R, 2R, and ALL, both within and over years (Table 3). In subset EARLY the GE-interaction was not significant in 1988, but was significant both in 1989 ($P < 0.001$) and when estimated over years.

Regression analysis of GE-interactions

The linear regression ($SS_{reg}/SS_{G \times E}$) explained 28–36% of the GE-interactions in subset EARLY, 26–40% in subset 6R, 27–38% in subset 2R, and 20–52% in subset ALL (Table 3). When regression mean squares were tested against the error mean squares, as shown by the F-values in Table 3, the level of significance was generally high ($P < 0.01$), except for subset 6R in 1989. Testing of the regression mean squares against the deviation mean squares, ($MS_{reg}/MS_{res.}$) demonstrated that the linear regression explained the GE-interactions well, i.e. the heterogeneity of regressions was significant among years in subset EARLY, for the year 1987 in subsets 6R and ALL, and over years in subsets EARLY and 6R.

Table 2 Average grain yields (kg/ha) of subsets within and among different locations and years

Entry	Year	EARLY	6R	2R	LATE	ALL
Hϕjbakkegård	87	–	1357	2466	2287	2108
	88	2945	3221	4199	4092	3883
	89	3209	3329	4535	4354	4146
Korpa	88	1745	–	–	–	–
	89	1258	–	–	–	–
Röbäcksdalen	88	2018	–	–	–	–
	89	2893	–	–	–	–
Svalöv	87	–	4116	4304	4283	4244
	88	4834	4952	5486	5420	5314
	89	4764	4696	5805	5599	5447
Viikki	87	–	3922	4033	4040	3998
	88	3353	3885	4421	4447	4248
	89	4388	4642	4306	4420	4415
Ås	87	–	5775	5619	5752	5669
	88	4027	4159	4333	4332	4277
	89	3076	3312	3549	3561	3473
Over years:						
Hϕjbakkegård		3077	2636	3733	3578	3379
Korpa		1501	–	–	–	–
Röbäcksdalen		2456	–	–	–	–
Svalöv		4799	4588	5198	5101	5002
Viikki		3871	4150	4254	4302	4220
Ås		3551	4415	4500	4548	4473
Over locations:	87	–	3792	4106	4090	4005
	88	3153	4054	4610	4573	4430
	89	3265	3995	4549	4483	4370
Grand mean		3209	3947	4421	4382	4268

Correlations between yield, b_i and λ_i, origin, row type and year of release

These correlations have been reported earlier for subsets EARLY, 6R, and 2R (Nurminiemi et al. 1996). When subsets LATE and ALL were included in the analyses many of the earlier results were confirmed. The regression coefficients were not correlated with Tai's λ_i-values (Table 4). 6r-lines were more responsive than 2r-lines, as shown by the correlation between b_i and row type which was $r = 0.42$ and 0.616 in subset LATE and ALL, respectively. However, 6r-lines gave lower yields than 2r-lines ($r = -0.378$ and -0.553 between yield and row type in subset LATE and ALL, respectively), and this resulted in grain yield being negatively correlated with responsiveness (b_i) ($r = -0.205$ and -0.361 for the two subsets).

Origin was assigned in a north-south direction so that Iceland, Finland, Norway, Sweden, and Denmark were given values from 1 to 5, respectively. Most of the responsive 6r-material came from Finland and Norway, while the majority of high-yielding 2r-barleys originated from Denmark and Sweden. This resulted in a negative correlation between b_i and origin, and between origin and row type, while grain yield and origin were positively associated. Newly bred barley lines yielded more than older varieties.

Among late-maturing lines the plant materials originating from the southern locations were more stable than those of northern origin ($r = -0.232$ between λ_i and origin). λ_i-values were positively correlated with row type which means that 6r-lines were more unstable than 2r-lines at the four southern locations.

Repeatability measured by means of the correlations between the response (b_i), the stability parameter (λ_i) and yield

The regression coefficients were correlated among years in subsets EARLY, LATE and ALL, but the direction of the correlations was inconsistent (Table 5). Regression coefficients estimated on location means over years were highly correlated with estimates based on location × year means ($r = 0.91$ in subset EARLY, $r = 0.43$ to 0.63 in subset 6R, and $r = 0.24$ to 0.49 in subset 2R; data not shown). Yield stability had even lower repeatability than responsiveness, and only the late-maturing material had partly similar λ_i-values in 1988 and 1989. λ_i's estimated from regression on location means over years were significantly correlated with λ_i's estimated from regression on location × year means ($r = -0.59$ and 0.78 in subset EARLY, $r = 0.30$ to 0.49 in subset 6R, and $r = 0.22$ to 0.55 in subset 2R; data not

Table 3 Results from the analyses of variance for the subsets EARLY, 6R, 2R, and ALL. An approximate *F*-test, $\text{MS}_{\text{reg.}}/\text{MS}_{\text{dev.}}$, shows whether the lines have reacted differently over environments

Year	Entries	EARLY			6R			2R			ALL		
		df	MS[a]	*F*	*df*	MS	*F*	*df*	MS	*F*	*df*	MS	*F*
1987	Env.				3	472 580		3	499 017		3	942 463	
	Genot.				70	1537		148	1229		219	3327	
	G × E				210	430	2.62***	444	334	2.53***	657	497	3.48***
	Regr.				70	521	3.18***	148	358	2.71***	219	780	5.45***
	Dev.				140	384	2.34***	296	322	2.45***	438	356	2.49***
	Error				280	164		592	132		876	143	
	$\text{MS}_{\text{reg}}/\text{MS}_{\text{dev}}$						1.36*			1.11 ns			2.19***
1988	Env.	5	111 180		3	72 879		3	104 119		3	166 759	
	Genot.	39	529		70	1018		148	973		219	5944	
	G × E	195	225	1.23 ns	210	319	1.92***	444	203	1.71***	657	287	1.98***
	Regr.	39	340	1.86***	70	339	2.04***	148	229	1.93***	219	246	1.69***
	Dev.	156	197	1.08 ns	140	309	1.86***	296	190	1.60***	438	308	2.12***
	Error	234	183		280	166		592	119		876	145	
	$\text{MS}_{\text{reg}}/\text{MS}_{\text{dev}}$			1.73**			1.10 ns			1.21 ns			0.80 ns
1989	Env.	5	123 371		3	86 120		3	261 806		3	295 854	
	Genot.	39	1050		70	1103		148	1165		219	6453	
	G × E	195	350	2.05***	210	353	1.49***	444	458	1.72***	657	660	2.55***
	Regr.	39	492	2.89***	70	278	1.18 ns	148	379	1.42**	219	404	1.56***
	Dev.	156	315	1.85***	140	392	1.66**	296	498	1.87***	438	788	3.04***
	Error	234	170		280	236		592	267		876	259	
	$\text{MS}_{\text{reg}}/\text{MS}_{\text{dev}}$			1.56*			0.71 ns			0.76 ns			0.51 ns
Over years	Env.	5	210 759		3	339 520		3	331 254		3	604 179	
	Genot.	39	1316		70	46500		148	91357		219	3886	
	G × E	195	400	2.21***	210	516	2.09***	444	403	1.78***	657	744	2.91***
	Regr.	39	725	4.00***	70	592	2.40***	148	323	1.43***	219	678	2.65***
	Dev.	156	318	1.76***	140	478	1.94***	296	443	1.96***	438	777	3.04***
	Error	702	181		1400	247		2960	226		4380	255	
	$\text{MS}_{\text{reg}}/\text{MS}_{\text{dev}}$			2.28***			1.24*			0.73 ns			0.87 ns

[a] Values of mean squares must be multiplied by 10^3

shown). Grain yield was highly repeatable in every subset ($r = 0.57$ to 0.85), and mean yield estimated on locations over years was highly correlated with the mean yield estimated on a location × year basis ($r = 0.86$ to 0.95, data not shown).

In subset LATE the b_i-values in 1987 were positively correlated with λ_i-values in 1988 and 1989, i.e. those genotypes which were responsive in 1987 were among the most unstable lines in 1988 and 1989. The situation was changed for genotypes that were responsive in 1989, which seemed to be more stable in 1988 and 1989 than less-responsive genotypes. When row types were tested separately, there was no relationship between responsiveness and yield stability (subsets 6R and 2R), except that 2r-lines that were responsive in 1987 were more unstable in 1989. Early maturing material showed the strongest association between b_i's and λ_i in 1989 ($r = -0.41$ and -0.44).

The correlation between grain yield and responsiveness varied from $r = -0.35$ to 0.62. Therefore, it seems possible to combine high yield with the desired responsiveness. Grain yield was positively correlated with yield stability only in subset 6R in 1988. Otherwise, associations were either non-significant or negative, indicating that high yield can be combined at least with average stability.

The highest- and lowest-yielding varieties in different subsets

Table 6 shows the behaviour of the five highest- and the five lowest-yielding accessions within each subset. Deviations from linear regression were often large, and only a few cultivars combined high yield with a stable performance. The Icelandic material was different from all others by exhibiting low yield capacity and low response to improved growing conditions. The large change in responsiveness and yield stability of the 6r 'Sigur-F' and 'Tampar', depending on the number of environments and genotypes included in the tests (subsets EARLY, 6R and ALL), is remarkable. This background effect was not as large for the Icelandic 2r-lines which were consistently low in response (subsets 2R and ALL).

In subset 2R 'Robert' was responsive, but not in subset ALL due to the changes in the group of reference genotypes. The highest-yielding variety 'Golf' originates from England, and the instability in this line was most probably caused by climatic effects of testing at higher latitudes. Crossings between different 6r- and 2r-barleys have resulted in variation both in responsiveness and stability (6r-line '77082', 2r-line '78133', and 2r 'Arla').

Table 4 Correlations between responsiveness (b_i), phenotypic stability (λ_i), mean yield, origin, year of release, and row type within different subsets

Subset		λ_i	Yield	Origin	Release	Row
LATE	b_i	0.031	−0.205**	−0.313***	−0.191	0.420***
	λ_i		−0.020	−0.232**	0.125	0.607***
	Yield			0.605***	0.552***	−0.378***
	Origin				0.114	−0.490***
	Release					−0.027
ALL	b_i	0.015	−0.361***	−0.413***	−0.191	0.616***
	λ_i		−0.003	−0.089	0.185	0.339***
	Yield			0.670***	0.499***	−0.553***
	Origin				0.140	−0.574***
	Release					−0.099

Significance of correlation at $P < 0.05$ = *, at $P < 0.01$ = **, and at $P < 0.001$ = ***

Table 5 Correlations between responsiveness (b_i), phenotypic stability (λ_i), and mean yields (Y) within different subsets and experimental years (1987–89)

Entry	Subset	Entry							
		b_i 88	b_i 89	λ_i 87	λ_i 88	λ_i 89	Y87	Y88	Y89
b_i 87	6r	−0.03	0.08	0.09	0.05	0.08	0.62***	0.38***	0.36**
	2r	0.11	0.10	0.04	0.09	0.21*	0.34***	0.27***	0.22**
	Late	0.02	−0.43***	0.06	0.28***	0.42***	0.08	−0.16*	−0.22**
	All	0.19**	−0.36***	0.05	0.29***	0.29***	0.06	−0.23***	−0.23***
b_i 88	Early		0.74***		0.14	−0.44**		0.33**	0.37*
	6r		0.18	0.01	−0.11	−0.16	−0.13	−0.35**	0.01
	2r		0.06	−0.08	0.02	−0.06	−0.21*	0.18*	0.13
	Late		0.08	−0.13	−0.002	−0.16*	0.15*	0.15*	0.10
	All		0.03	0.01	0.22***	−0.11	0.04	−0.16*	−0.07
b_i 89	Early				0.04	−0.41**		0.37*	0.58***
	6r			0.01	−0.03	−0.01	−0.16	−0.20	0.07
	2r			−0.12	−0.08	−0.03	0.32***	0.35***	0.39***
	Late			−0.07	−0.25***	−0.24**	0.29***	0.45***	0.51***
	All			−0.07	−0.14*	−0.10	0.24***	0.35***	0.43***
λ_i 87	6r				0.07	0.03	0.02	−0.04	0.003
	2r				0.02	0.15	−0.16	−0.20*	−0.25**
	Late				0.09	0.08	−0.07	−0.10	−0.16*
	All				0.06	−0.06	−0.07	−0.16*	−0.17*
λ_i 88	Early					0.09		0.14	0.12
	6r					0.02	0.13	0.31**	0.21
	2r					0.15	−0.01	−0.05	−0.01
	Late					0.22**	−0.05	−0.13	−0.17
	All					0.11	0.02	−0.12	−0.09
λ_i 89	Early							−0.33*	−0.41**
	6r						0.19	0.20	0.20
	2r						−0.06	−0.17*	−0.16
	Late						−0.03	−0.19*	−0.17*
	All						0.05	−0.04	−0.005
Y87	6r							0.64***	0.57***
	2r							0.70***	0.62***
	Late							0.65***	0.57***
	All							0.72***	0.66***
Y88	Early								0.71***
	6r								0.69***
	2r								0.81***
	Late								0.80***
	All								0.85***

Table 6 Mean grain yield, responsiveness (b_i), and phenotypic stability (λ_i) for the 5 highest (top) and the 5 lowest (bottom) yielding cultivars within each subset

Subset	C[a]	Name	Yield	b_i[b]	λ_i
EARLY	F	Silja	3556	1.15	1.6
	N	M-268	3522	1.07	1.1
	N	Vo-H-10660	3470	0.97	4.3
	N	Agneta	3451	1.08	0.2
	F	1279	3417	0.92	1.5
	N	H-349-10	3022	1.01	4.6
	I	046	3005	0.63 + +	1.1
	F	Hja-673	2999	0.97	1.7
	I	Tampar	2811	0.95	0.7
	I	Sigur-F	2227	0.36 +	5.2
6R	N	H-1027	4889	0.81	2.8
	N	H-1014	4433	0.88	3.8
	F	77082	4391	1.26*	0.3
	N	Vo-H-2912	4382	0.88	5.2
	F	1374	4341	0.62	2.6
	F	78023	3599	0.70	8.6
	N	Varde	3587	0.90	1.3
	N	M-65	3479	1.08	2.2
	I	Tampar	3050	0.78	4.0
	I	Sigur-F	2396	0.75	0.9
2R	S	Golf	5057	1.26	4.8
	S	80512	4030	0.77	1.1
	S	Robert	4939	1.23**	0.01
	S	Benedicte	4886	0.71	1.2
	S	Lina	4877	0.91	0.2
	S	Arla	3579	1.22	0.4
	F	78133	3558	1.05	18.5
	I	046	3235	0.64 +	0.4
	I	051	3136	0.65 +	0.3
	I	054	3043	0.69	2.0
ALL	S	Golf	5057	0.99	9.0
	S	80512	5030	0.70	0.8
	S	Robert	4939	1.08	0.8
	N	H-1027	4889	1.11	1.5
	S	Benedicte	4886	0.61	1.7
	I	046	3235	0.57 + +	0.3
	I	051	3136	0.55	0.9
	I	Tampar	3050	1.10	1.3
	I	054	3043	0.61	2.0
	I	Sigur-F	2396	1.02	0.2

[a] C = Country of origin of seed sample: I = Iceland, F = Finland, N = Norway and S = Sweden.

[b] b_i is significantly > 1, at $P < 0.05$ = *, and at $P < 0.01$ = **
b_i is significantly < 1, at $P < 0.05$ = +, and at $P < 0.01$ = + +

Pedigree studies of responsiveness

The results demonstrate significant differences in responsiveness among closely related breeding lines. In subset 6R, the line '78003' originated from the backcross 'Hiproly/2* Hankkija-673', and was significantly less responsive than 'Hankkija-673' ($b_{78003} = 1.01 \pm 0.06$ and $b_{\mathrm{Hankkija-673}} = 1.22 \pm 0.03, P < 0.025$). This is probably caused by the incorporation of the less-adapted Ethiopean 'Hiproly'-barley in the genetic background. However, '78003' outyielded its backcross parent by 19%. Another example (in subset ALL) of recombination between different alleles from the parents is exhibited by the Danish line '602216', which originates from the cross 'Nordal × Triumph'. Line '602216' was responsive, ($b_{602216} = 1.35 \pm 0.04$), while 'Nordal' was not responsive ($b_{\mathrm{Nordal}} = 0.63 \pm 0.13$), and they reacted significantly differently ($P < 0.005$). 'Triumph' was also rather non-responsive (two different accessions, $b_{\mathrm{Triumph1}} = 0.82 \pm 0.42$ and $b_{\mathrm{Triumph2}} = 0.76 \pm 0.32$) but, due to high standard errors of the regression coefficients, the difference between b_{602216} and b_{Triumph1} or b_{Triumph2} was not significant.

Discussion

The number of genotypes tested in every subset was large enough to give reliable estimates of environmental indices. The success of the regression method in explaining GE-interaction in subset EARLY was due to the wider range, and a more even distribution, of experimental locations as compared to other subsets, which were tested at fewer locations (Table 2). Also the 40 early maturing genotypes were very different in their response to the growing conditions. The number of locations and the range in productivity of the four southern locations, where 2r-barleys were tested, were not large enough to differentiate the response patterns among genotypes, as evidenced by the non-significant regression mean squares.

The 2r-lines yielded more, and had a more similar performance among test locations, than the 6r-lines, which exhibited a differential response to the atypical growing conditions for 6r-barleys in southern Scandinavia. This can be partly explained by the stronger daylength response of 6r-lines (Wiberg 1993), and the better adaptation, e.g. disease and lodging resistance, of 2r-lines (data not shown).

The results demonstrate that the regression coefficients are very vulnerable to changes in the number of environments, and the reference group of genotypes (subsets EARLY and 6R), or even to changes of reference groups of genotypes only (subsets 6R vs ALL and 2R vs ALL). However, responsive genotypes identified in subsets 6R and 2R were not less responsive in subset ALL, but linearity was lost when the two different row types were analyzed together. Therefore, 2r- and 6r-materials should be tested separately due to their different intensity of response to the changing growing conditions in the Nordic countries. Grouping of material by earliness would identify stable genotypes within different maturity groups. In this way factors causing instability, e.g. unfavourable weather conditions at a certain physiological growth stage, could more easily be detected.

Regression coefficients estimated on location means over years are easier to interpret than b_i's estimated on location × year means (Becker 1984). If the regression sum of squares explain most of the GE-interaction, and GL-interaction is higher than GY- and/or GLY-interactions, then b_i has a predictable value. In this case the b_i's can be used to predict the expected yield response of genotypes in the actual range of environments. This was the case in subset EARLY, where the GL-interaction component of grain yield was the most important interaction component (Nurmimiemi et al. 1996).

Léon and Becker (1988) showed that single-year estimates of the deviations from regression (S^2_{di}) had a very low repeatability when genotype × year (GY), and genotype × location × year (GLY) interactions were large, even if the number of locations was high (16) for spring barley. Several studies have shown that S^2_{di} is not consistently associated with b_i or the mean yield (Perkins and Jinks 1968b; Langer et al. 1979; Pham and Kang 1988; Yue et al. 1990; Jalaluddin and Harrison 1993). We also found that neither responsiveness nor yield stability were consistently correlated with grain yield. Therefore, b_i and grain yield are at least partly independent and presumably subject to the control of different genetic systems (Perkins and Jinks 1968b; Langer et al. 1979; Becker 1981, 1983). It should therefore be possible to combine high-yielding ability with the desired level of responsiveness. In addition, cultivars with small deviations from the predicted response, i.e. stable varieties, can be selected.

The mean performance of genotypes is often the only measurement of environmental productivity that can be obtained, since adequate physical or biological characteristics of environments are difficult to estimate. Repeatability of S^2_{di} is low, irrespective of it being estimated on location means (over years) or on location × year means. However, the latter can be used as a stability parameter for the more unpredictable location × year variation, and for the recommendation of regionally adapted cultivars. More attention should be paid to the sign and amount of deviation at different locations instead of the squared sums of deviations. High and positive deviations from regression at some locations reveals that the genotype has higher adaptability to these specific growing conditions than the average of the whole material. This is often the case with resistance to biotic or edaphic factors that limit plant growth.

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References

Aastveit AH (1977) Statistical analyses of field trials with a large number of entries. Thesis, Mathematical Statistics, University of Oslo (in Norwegian)

Allard RW, Bradshaw AD (1964) Implications of genotype-environmental interactions in applied plant breeding. Crop Sci 4:503–508

Allen FL, Comstock RE, Rasmusson DC (1978) Optimal environments for yield testing. Crop Sci 18:747–751

Austin RB (1988) A different ideotype for each environment? In Jorna ML, Slootmaker LAJ (eds) Cereal breeding related to integrated cereal production. EUCARPIA Proc Conf Cereal Section, Pudoc, Wageningen, pp 47–60

Becker HC (1981) Biometrical and empirical relations between different concepts of phenotypic stability. In: Gallais A (ed) Quantitative genetics and breeding methods. EUCARPIA Proc 4th Meet Section Biometrics Plant Breeding, 2–4 September 1981, Poitiers, France. INRA, Versailles, pp 307–314

Becker HC (1983) Züchterische Möglichkeiten zur Verbesserung der Ertragssicherheit. Vortr Pflanzenzüchtg 3:203–225

Becker HC (1984) Analysis of genotype × environment interactions with partitioning of environmental effects into effects of locations and years. Vortr Pflanzenzüchtg 7:209–218

Becker HC, Léon J (1988) Stability analysis in plant breeding. Plant Breed 101:1–23

Ceccarelli S, Grando S (1991) Selection environment and environmental sensitivity in barley. Euphytica 57:157–167

Eberhart SA, Russell WA (1966) Stability parameters for comparing varieties. Crop Sci 6:36–40

Finlay KW, Wilkinson GN (1963) The analysis of adaptation in a plant-breeding programme. Aust J Agric Res 14:742–754

Jalaluddin Md, Harrison SA (1993) Repeatability of stability estimators for grain yield in wheat. Crop Sci 33:720–724

Knight R (1970) The measurement and interpretation of genotype-environment interactions. Euphytica 19:225–235

Langer I, Frey KJ, Bailey T (1979) Associations among productivity, production response, and stability indexes in oat varieties. Euphytica 28:17–24

Léon J, Becker HC (1988) Repeatability of some statistical measures of phenotypic stability – correlations between single-year results and multi-year results. Plant Breed 100:137–142

Lin CS, Binns MR (1988) A method of analyzing cultivar × location × year experiments: a new stability parameter. Theor Appl Genet 76:425–430

Lin CS, Binns MR (1991) Assessment of a method of cultivar selection based on regional trial data. Theor Appl Genet 82:379–388

Nilsen J (1983) Light climate in northern areas. In Kaurin Å, Junttila O, Nilsen J (eds) Plant production in the north. Norwegian University Press, pp 62–72

Nissilä E (1992) Yield stability parameters of barley under Finnish conditions. Acta Agric Scand, Sect B, Soil and Plant Sci 42:152–157

Nurminiemi M, Bjφrnstad Å, Rognli OA (1996) Yield stability and adaptation of Nordic barleys. Euphytica (in press)

Perkins JM, Jinks JL (1968 a) Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. Heredity 23:339–356

Perkins JM, Jinks JL (1968b) Environmental and genotype-environmental components of variability. IV. Non-linear interactions for multiple inbred lines. Heredity 23:525–535

Pfeiffer WH, Braun HJ (1989) Yield stability in bread wheat. In: Anderson JR, Hazell PBR (eds) Variability of grain yields. Implications for agricultural research and policy in developing countries. John Hopkins, University Press, Baltimore, pp 157–174

Pham HN, Kang MS (1988) Interrelationships among and repeatability of several stability statistics estimated from international maize trials. Crop Sci 28:925–928

Reysack JJ, Stuthman DD, Stucker RE (1993) Recurrent selection in oat: stability of yield and changes in unselected traits. Crop Sci 33:919–924

Shabana R, Bailey T, Frey KJ (1980) Production traits of oats selected under low, medium, and high productivity. Crop Sci 20:739–744

Simmonds NW (1991) Selection for local adaptation in a plant breeding programme. Theor Appl Genet 82:363–367

Skrφppa T (1984) A critical evaluation of methods available to estimate the genotype × environment interaction. Studia For Suec 166:3–14

SNP (1986) Samordnad odlingsvärdesprovning i Norden. SNP publikation nr. 14. Nordisk Ministerråd, Oslo, Norway

SNP (1992) Agroklimatisk kartlegging av Norden. Samnordisk planteforedling. Skrifter och rapporter nr 5. BTJ Tryck AB, Lund, Sweden

Tai GCC (1971) Genotypic stability analysis and its application to potato regional trials. Crop Sci 11:184–190

Wiberg A (1993) Norrländskt jordbruk – finns det behov av speciell sortframställning? Sveriges Utsädesf Tidskr 103:17–24

Yates F, Cochran, WG (1938) The analysis of groups of experiments. J Agric Sci 28:556–580

Yue G, Perng SK, Walter TL, Wassom CE, Liang GH (1990) Stability analysis of yield in maize, wheat and sorghum and its implications in breeding programs. Plant Breed 104:72–80