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Genetic gain and genetic diversity in German winter barley cultivars

J. Ahlemeyer*, F. Aykut*, W. Köhler*, W. Friedt* and F. Ordon**
*Institute of Agronomy and Plant Breeding, Research Centre for Bio Systems, Land Use and Nutrition,
Justus-Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany
**Institute of Epidemiology and Resistance Resources, Federal Centre for Breeding Research on
Cultivated Plants, Theodor-Roemer-Weg 4, 06449 Aschersleben, Germany

SUMMARY – During the last decades winter barley yield in Germany has increased by 72 kg per hectare and year. In order to determine the share of the genetic gain in this increase a set of 65 six-rowed and 52 two-rowed cultivars that were registered in Germany during the last 40 years were screened in 13-sited field experiments regarding yield and yield components as well as resistance to biotic and abiotic stresses. The annual genetic gain was estimated at 43 and 39 kg ha-1 for six- and two-rowed cultivars, respectively, accounting for about 50% of the increase estimated on farmers' fields. At the same time the genetic diversity as determined on the basis of 70 SSRs slightly decreased in the six-rowed cultivars and considerably increased in the two-rowed cultivars. First results for marker-trait associations detected between SSR loci and agronomically important traits are shown.

Introduction

Advances in plant breeding together with improvements in plant production have led to an average annual increase of 72 kg ha^{-1} in winter barley yield in Germany during the last five decades (Fig. 1). In order to specify the share of the genetic gain in this improvement, 65 six-rowed and 52 two-rowed winter barley cultivars, that were registered in Germany during the last four decades and gained certain importance during that time, were analysed in a 13-sited field experiment. In addition to grain yield and yield components like the number of ears/m², grains per ear and thousand grain weight, the resistance of these cultivars against plant diseases and lodging were investigated. Simultaneously a genotypic characterisation of the 117 winter barly cultivars was carried out by means of 70 genome-wide SSRs (simple sequence repeats) in order to determine the genetic diversity and to associate phenotypic traits to specific genomic regions.

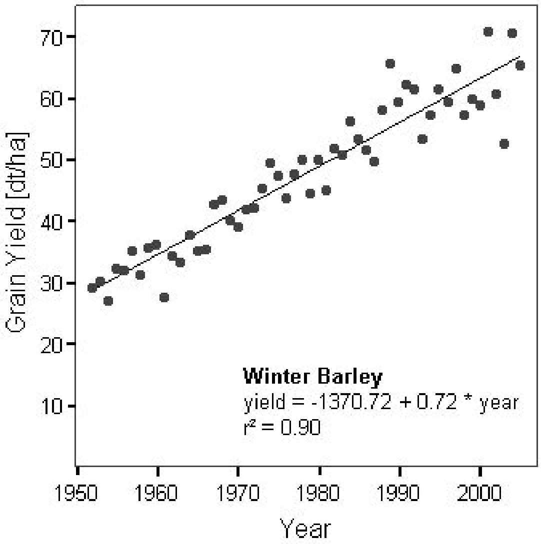

Fig. 1. Increase in winter barley yield in Germany between 1952 and 2005. Data are based on the Special Yield Enquiry of the Federal Statistical Office, Germany.

Material and methods

Plant Material: 65 six-rowed and 52 two-rowed winter barely cultivars were selected taking into account the acreage covered during recent decades and their importance as parents in breeding programs. The six-rowed cultivars chosen were registered between 1959 and 2003, the two-rowed cultivars between 1968 and 2003.

Field Experiments: Field experiments were conducted in cooperation with private breeding companies at 13 different sites in Germany and designed according to an Alpha-lattice with two replications per site. The number of ears/m² was determined by counting the number of tillers of one meter of a row and converting this value to one square meter of the plot. The number of grains per ear was determined by dividing the grain yield per plot by the grain weight and the number of spikes per plot. Lodging and diseases were scored on a 1 to 9 scale were 1 means no occurrence of symptoms and 9 means full development of symptoms.

SSR Analysis: DNA for SSR marker analysis was extracted from leaf material of three-week old plants using the CTAB method (Doyle and Doyle 1990). 70 SSR primer combinations that cover the barley genome evenly were selected and PCR reactions were performed according to Ramsay *et al.* 2000. Banding patterns were visualised using a LI-COR DNA sequencer.

Data Analysis: Data obtained in the field experiments were analysed using the procedure MIXED of SAS (Version 8.02). The least square means for all six- and two-rowed cultivars, respectively, were regressed on the years of release and the regression coefficient (b) was taken as an estimate for the genetic gain in the respective trait. The genetic diversity (DI) within groups of cultivars was calculated according to Nei (1973). A principle coordinate analysis (PCoA) based on Dice's similarity coefficient was conducted using NTSYS-PC (Version 2.20e). Additionally the population structure was analysed by means of a Bayesian approach on basis of 14 SSRs that are located on the outer chromosome arms using the software STRUCTURE (Pritchard *et al*., 2000). Associations were calculated for six- and two-rowed cultivars separately by means of one-way GLMs with the least square means of thousand grain weight and lodging as criterion variable and the respective SSR as factor using the software TASSEL (Version 1.9.4). A Bonferroni correction was applied to keep the experiment-wise error rate at less then 5%.

Results and discussion

Genetic gain in yield and yield components

In six-rowed as well as in two-rowed cultivars grain yield and the year of release of the cultivars were highly correlated (Table 1) with coefficients of determination of 50.4 and 66.9, respectively. On average, the yield for six-rowed cultivars increased by about 43 kg ha^{-1} per year and by about 39 kg ha^{-1} for the two-rowed cultivars. Even if these values might be slightly overestimated, because all cultivars were tested using the same modern plant production measures, the genetic gain clearly accounts for more than 50 % of the increase in yield achieved on farmers fields.

Although the genetic gain in grain yield is comparably high for six-rowed and two-rowed cultivars the genetic gain in yield components differs between both populations. While the increase in yield is mainly due to an increased number of ears/m² for the two-rowed cultivars, the six-rowed cultivars show a highly significant gain in thousand grain weight (Table 1).

Genetic gain in resistance to pathogens and lodging

Apart from yield and yield components, different traits influencing yield stability were monitored in the field experiments. For six-rowed as well as for two-rowed cultivars the scores for lodging showed a highly significant negative correlation with the year of release (Table 2). For the six-rowed cultivars released before 1985 the median score was 6.0 while for the cultivars released later than 1995 the median score was 1.8. Compared to lodging the median scores for awn kinking show smaller differences between older and newer cultivars. Nevertheless, the correlations with the year of release are negative for both populations. Improvements in breeding for disease resistance are especially evident for powdery mildew resistance in the six-rowed cultivars, while for scald only a tendency for a higher level of resistance in the newer cultivars was found.

Table 1. Genetic gain in grain yield and in yield components. Given are the number of sites under investigation, the genetic gain estimated as the coefficient (b) of the regression of the trait on the year of release, the respective correlation coefficient (r) and its p-value as well as the relative and absolute increase from 1959 to 2003 for six-rowed and from 1968 to 2003 for two-rowed winter barley cultivars

		# sites	Genetic gain (b)	r	p	Relative increase	Absolute increase
Grain yield	Six-rowed	12	43.2 [kg ha^{-1} y^{-1}]	0.710	< 0.001	27 %	19.0 [kg ha^{-1}]
	Two-rowed	13	39.1 [kg ha^{-1} y^{-1}]	0.818	< 0.001	20 %	13.7 [kg ha^{-1}]
Number of spikes	Six-rowed	8	-0.29 [m^{-2} y^{-1}]	-0.078	0.539	-2 %	-12.6 [m^{-2}]
	Two-rowed	9	3.06 [m^{-2} y^{-1}]	0.350	0.012	14 %	107.3 [m^{-2}]
Grains per spike	Six-rowed	7	0.02 [y^{-1}]	0.075	0.554	2 %	0.8
	Two-rowed	8	0.01 [y^{-1}]	0.034	0.812	1 %	0.2
Thousand grain weight	Six-rowed	10	0.22 [g y^{-1}]	0.604	< 0.001	27 %	9.7 [g]
	Two-rowed	12	0.07 [g y^{-1}]	0.163	0.253	5 %	2.4 [g]

Table 2. Genetic gain in resistance to lodging and diseases. Given are the medians of scores monitored on a 1 to 9 scale for cultivars released earlier than 1985, between 1985 and 1995 and after 1995 as well as the rank correlation coefficient (r_s) and its p-value for the correlation between year of release and median of the score

		# sites	< 1985	1985 - 1995	> 1995	r_s	p
Lodging	Six-rowed	7	6.0	4.6	1.8	-0.819	< 0.001
	Two-rowed	7	3.7	2.2	1.5	-0.510	< 0.001
Awn kinking	Six-rowed	3	3.0	2.5	2.5	-0.206	0.099
	Two-rowed	5	3.0	3.0	2.0	-0.311	0.026
Powdery mildew	Six-rowed	3	6.0	5.0	4.0	-0.582	< 0.001
	Two-rowed	3	2.6	2.8	2.0	-0.149	0.296
Scald	Six-rowed	3	2.3	2.0	2.0	-0.167	0.183
	Two-rowed	3	2.0	2.0	1.5	-0.193	0.175

Genetic diversity and its development over time

A principle coordinate analysis on the basis of 70 SSRs (Fig. 2) showed a clear cut separation of six-rowed and two-rowed cultivars on the first axis which accounts for 16 % of the total genetic variation between cultivars. Within the six-rowed and the two-rowed cultivars the genetic diversity (DI, Nei 1973) was estimated at DI = 0.418 and DI = 0.419, respectively. However, for the six-rowed cultivars a slight decrease of the genetic diversity over time was found, while for the two-rowed cultivars a considerable increase was detected. This might be a consequence of the intense breeding efforts made for two-rowed winter barley cultivars in Germany during recent decades (Table 3).

Associations of SSRs with grain weight and lodging

For the two important traits thousand grain weight and lodging the phenotypic and genotypic diversity within the cultivars was used to detect marker trait associations. In order to avoid spurious associations a refined analysis of the population structure was carried out on basis of unlinked markers. This analysis supported the findings of the PCoA analysis that the 117 cultivars can be divided into two subpopulations on basis of the number of kernel rows. At an experiment-wise error rate of 5 % significant associations of markers with thousand grain weight were only found for the six-rowed cultivars on chromosome 3H mapping at 54 to 55 cM on the map of Ramsay *et al*. (2000; Table 4). Associations for lodging were found for both six-rowed and two-rowed cultivars on chromosome 5H. One additional marker associated with lodging was found for both six-rowed and two-rowed cultivars on 3H and 2H, respectively.

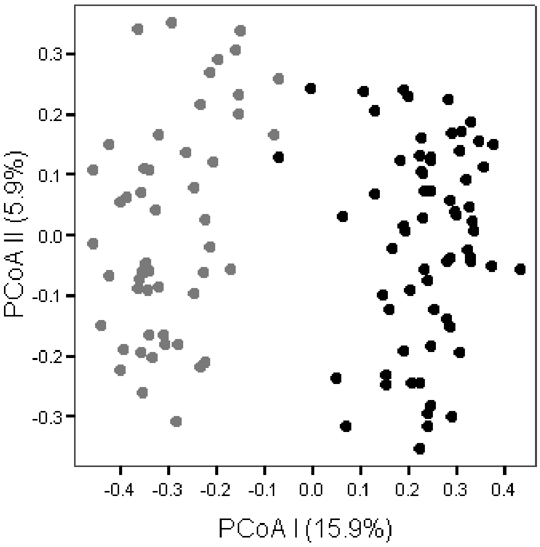

Fig. 2. PCoA with 65 six-rowed (black) and 51 two-rowed (grey) winter barely cultivars on the basis of 70 SSRs.

Table 3. Genetic diversity (DI, Nei 1973) in relation to the year of release

Year of release	DI six-rowed	DI two-rowed
< 1985	0.406	0.309
1985 - 1995	0.406	0.404
> 1995	0.385	0.421
total	0.418	0.419

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Table 4. SSR-markers associated with thousand grain weight and lodging, respectively. Only markers with associations significant on an experiment-wise error rate of 5% either in the six-rowed or/and the two-rowed cultivars are given (respective p-values are indicated with*). For these markers data are shown for both six-rowed and two-rowed cultivars including the number of cultivars carrying the allele and the respective mean. Means sharing the same letter are not significantly different

Position	SSR	Allele	Six-rowed cultivars				Two-rowed cultivars			
			n	Mean		p	n	Mean		p
Thousand grain weight										
3H 54 cM	Bmac0067	171	22	41.0	a	< 0.001*	8	51.8	a	0.321
		175	36	44.7	b		30	53.5	a	
		177	5	44.1	b		10	54.3	a	
3H 54 cM	Bmag0006	169	35	44.8	a	< 0.001*	-	-	-	0.228
		171	25	41.1	b		23	53.0	a	
		175	5	44.1	ab		26	54.2	a	
3H 55 cM	Bmac0209	174	4	43.6	ab	< 0.001*	26	54.4	a	0.171
		189	37	44.8	a		-	-	-	
		191	22	40.7	b		25	53.0	a	
Lodging										
2H 63 cM	Bmag0125	118	20	3.77	a	0.901	2	2.00	ab	< 0.001*
		132	35	3.99	a		4	1.55	a	
		135	-	-	-		19	1.91	a	
		136	3	4.27	a		12	2.39	ab	
		137	-	-	-		8	3.54	b	
3H 74 cM	Bmag0225	143	31	2.90	a	< 0.001*	-	-	-	0.731
		145	10	5.79	b		5	1.88	a	
		147	21	4.75	b		4	2.63	a	
		157	-	-	-		3	2.17	a	
		164	-	-	-		14	2.16	a	
5H 35 cM	Bmag0394	171	16	5.66	a	< 0.001*	4	3.83	a	< 0.001*
		175	12	4.21	ab		-	-	-	
		177	36	3.28	b		45	2.14	b	

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