Heritability of Indirect Bread-making Quality Traits in Segregating Generations of Two Winter Wheat Crosses

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Summary

Modern wheat breeding programs aim to create cultivars with high genetic potential for yield and bread-making quality. The effectiveness of selection in segregating generations depends on the heritability of the traits under selection and on the correlations among traits. The aim of this study was to compare realized heritability of 1000 kernel weight and five indirect bread-making quality traits (grain protein content, wet gluten content, gluten index, the Zeleny sedimentation value and Pelshenke value) between segregating generations (F4 to F6) of two bi-parental wheat crosses, calculated using four different methods, and to estimate phenotypic correlations among these traits. Realized heritability of investigated traits, estimated as parent-offspring regression, ranged from 0.21 to 0.79. Realized heritability for wet gluten content, gluten index and Pelshenke value was much higher in comparison with other quality traits. Correlations between the four methods used to calculate realized heritability revealed the best agreement between heritability estimated as parent-offspring regression and that based on divergent screening, and the lowest agreement between realized heritabilities based on upward and downward screening. Strong positive correlations were observed among grain protein content, wet gluten content, and Zeleny sedimentation value; and strong negative correlations between gluten index on one side and grain protein content and wet gluten content on the other side.

Key words

winter wheat, yield, quality, heritability

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Introduction

Grain yield and grain quality are two major targets in wheat breeding programs, which determine the economic value of a wheat cultivar. However, it has been difficult to improve these two traits simultaneously due to the negative relationship between them (Noaman et al., 1990; Simmonds., 1995; Branlard et al., 2001; Monaghan et al., 2001; Oury and Godin, 2007). Therefore, a possible breeding strategy is to identify genotypes with favorable deviation from this relationship, as proposed by Monaghan et al. (2001), Oury and Grodin (2007) and Fossati et al. (2010). In addition to the correlation of yield and grain quality, correlations between different quality indicators are also important for practical breeding. Breeders use various tests to evaluate wheat grain quality, based on end-use quality objective of the breeding programs (Branlard et al., 1992). Quality parameters, which have often been used in breeding programs, include grain protein content, Zeleny sedimentation value and SDS sedimentation value, gluten content, gluten index, as well as Pelshenke value (Fisher et al., 1989; O' Brien and Ronalds., 1987; Branlard et al., 1992; Gras and O' Brien., 1992; Nishio et al., 2007). Previous studies have reported a positive correlation between protein content and wet gluten content within the range 0.71 to 0.90 (Gröger et al., 1997; Jurković et al., 2000; Mikulikova et al., 2009; Fossati et al.) as well as protein content and Zeleny sedimentation value or SDS sedimentation value, where the values ranged from 0.52 to 0.91 (Zeleny et. al., 1960; Parades-Lopez et al., 1985; Campbell et al., 1987; Fisher et al., 1989; Gröger et al., 1997; Jurković et al. 2000; Singht et al. 2015). However, gluten index as an indicator of the quality of gluten is generally negatively correlated with protein content, gluten content and sedimentation value (Parades-Lopez et al., 1985; Fisher et al., 1989; Jurković et al., 2000; Novoselović et al., 2012). Fisher et al. (1989) reported a positive correlation of Pelshenke value with protein content.

The effectiveness of selection for grain quality in early generations depends on the heritability of quality traits and on any unfavorable correlated response in other important characteristics, in particular grain yield (Fisher et al., 1989). Heritability of grain yield is generally much lower than for grain quality traits (Briggs and Shebeski, 1971; Ortiz et al., 2001).

In the experiments including inbred populations (lines and varieties), heritability for protein content ranged from 0.41 to 0.97 and for Zeleny sedimentation value from 0.50 to 0.98 (Bhatt and Derrera., 1975; O' Brien and Ronalds., 1987; Branlard et al. 1992; Denčić et al., 2001; Mladenov et al., 2001; Šarčević et al., 2014), but estimates of realized heritability in the selection experiments were generally lower ranging from 0.05 to 0.46 for protein content, and from 0.44 to 0.89 for SDS sedimentation value (Fisher et al., 1989; May et al., 1989; Nishio et al., 2005). Previous reports have focused on realized heritability of grain protein content, SDS sedimentation value as well as Pelshenke value, whereas realized heritabilities of Zeleny sedimentation value, wet gluten content and gluten index are poorly documented. In addition to that, despite of several available methods for calculating realized heritability, most studies were based just on single method so there is lack of information on agreement between different methods.

The aim of this study was to compare realized heritability of 1000 kernel weight and five indirect bread-making quality traits between segregating generations of two bi-parental wheat crosses, calculated using four different methods, and to estimate phenotypic correlations among these traits.

Materials and methods

The F4, F5 and F6 segregating generations of two bi-parental wheat crosses, Golubica × Emesse (G×E) and Verbunkos × Soissons (V×S), were grown at the experimental field of the Bc Institute Zagreb at location Botinec during seasons 2010/11, 2011/12 and 2012/13, respectively. The F4 lines were derived from individual F3 plants, whereas F5 and F6 lines were produced as seed bulks within lines from F4 and F5 generations, respectively. Fifty lines per cross were grown in non-replicated 0.7 m^2-plots for each of the three segregating generations. Agricultural practice was as commonly used in breeding experiments, except that fungicide treatment to control leaf and spike diseases were applied at the beginning of stem elongation and at flowering stage.

At maturity, all plots were harvested and grain yield and 1000 kernel weight (expressed on a 13% moisture basis) were determined. Bread-making quality of harvested grain was scored using grain protein content, wet gluten content, gluten index, Zeleny sedimentation value and Pelshenke value. The nitrogen percentage of dry grain was determined by the Kjeldahl method ICC No. 105/1 and grain protein content (GPC) was calculated by multiplying N percentage with conversion factor 5.83 (FAO 2003). Other indirect parameters as wet gluten content (WGC) and gluten index (GI) were determined according to ICC No. 155 on a Glutomatic 2200 (Perten Instruments AB, Sweden) and Zeleny sedimentation value (ZSV) according to ICC No 116. Pelshenke test was conducted according to AACC method 56-60 (1976).

Descriptive statistics (means, ranges and coefficients of variation) for all traits and Pearson's correlation coefficients among traits were calculated for all segregating generations using SAS software (SAS Institute Inc. 2003) by using UNIVARIATE and PROC CORR procedure, respectively. Realized heritability of investigated traits between successive generations was calculated according to Fehr et al. (1987) as the parent-offspring regression (h^2_b) and as the ratio of the observed selection response R to the observed selection differential S. The R and S values were calculated for the offspring and the parental generations, respectively, by assuming selection intensity of 20% in parental generation for both higher rank (upward screening) and lower rank (downward screening) of each trait. To estimate heritability of upward and downward screening, the R and S were calculated as the difference between high group mean and the whole population mean ($h^2_{high-average}$) and the difference between low group mean and the whole population mean ($h^2_{average-low}$), respectively. To estimate heritability of divergent screening R and S were calculated as the difference between high and low group means ($h^2_{high-low}$).

All heritability estimates were calculated based on standardized trait values (actual values divided by the corresponding standard deviations) to reduce the effects of environmental interactions for successive segregating generations that were grown in different years (Frey and Horner, 1957).

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Results and discussion

Descriptive statistics

Means, ranges and coefficients of variation (CV) for seven traits in three segregating generations of two wheat crosses Golubica × Emesse (G × E) and Verbunkos × Soissons (V × S) were shown in the Table 1. For both crosses, means for 1000 kernel weight were similar across all three segregating generations. On the other hand, means of all indirect quality traits except gluten index were considerably lower in F4 as compared to F5 and F6 generations. Analysis of variance (ANOVA) revealed significant differences between crosses for all traits except for grain protein content in F6, gluten index in F4, and Pelshenke value in F4 and F5 generations. The highest coefficients of variation in segregating generations of both crosses were observed for Pelshenke value (27.1% to 36.4%) and the lowest for grain protein content (3.4% to 7.6%).

Realized heritability

The h^2_b for 1000 kernel weight across generations and crosses ranged from 0.53 to 0.69 (Table 2). This is in agreement with results of Oliveira et al. (2012) whose heritability estimates for 1000 kernel weight between F3 and F4 generations of eight crosses ranged from 0.20 to 0.84 with an average of 0.59. Nishio et al. (2005) also reported high heritability estimates for 1000 kernel weight between F3 and F4 generations of two wheat crosses (0.60 to 0.81) by assuming selection intensity of 10% in both directions (upward and downward screening). Similarly, Briggs and Sibeski (1971) found relatively high estimates of realized heritability for 1000 kernel weight between F3 and F5 generations in

two populations (0.64 and 0.69), while in one population the heritability estimate was not significant. In the present study the h^2_b was moderate to high for wet gluten content (0.43 to 0.69), gluten index (0.55 to 0.76) and Pelshenke value (0.49 to 0.73), moderate for Zeleny sedimentation value (0.32 to 0.49) and low for protein content (0.21 to 0.40). Previous studies also reported lower realized heritability for protein content than for other quality traits depending upon the progeny studied and the method used in calculating the heritability. For protein content it ranged from 0.05 to 0.49, for SDS sedimentation value from 0.44 to 0.89, and for Peleshenke value from 0.50 to 0.77 (O' Brien and Ronalds., 1987; Fisher et al., 1989; May et al., 1989; Nishio et al., 2007).

Realized heritability estimated from divergent screening ($h^2_{high-low}$) had in most cases similar values as h^2_b (Table 2). The values of other two estimators of realized heritability ($h^2_{high-average}$ and $h^2_{average-low}$) were generally much lower or much higher in comparison to h^2_b and $h^2_{high-low}$. The best agreement between values of h^2_b and $h^2_{high-low}$ is confirmed by the highest correlation between them, which over crosses and generations ranged from 0.87 to 0.98 (Table 3). The lowest correlations were determined between $h^2_{high-average}$ and $h^2_{average-low}$ (-0.03 to 0.75). Nishio et al. (2005) compared two estimators of realized heritability, one based on downward screening and the other based on upward screening, for 1000 kernel weight, protein content and SDS sedimentation value from F3 to F4 generation of two wheat crosses. In their study, SDS sedimentation value showed higher heritability in downward screening, whereas protein content showed higher heritability in upward screening. On the other hand, heritability of 1000 kernel weight was higher in

Table 1. Means for 1000 kernel weight and indirect quality traits for the crosses Golubica × Emesse (G×E) and Verbunkos × Soissons (V×S)

	G×E			V×S			G×E vs. V×S
	Range	Mean	CV (%)	Range	Mean	CV (%)	ANOVA
			1000 kernel weight (g)				
F4	41.3-63.7	48.2	8.1	35.0-52.0	44.8	7.1	**
F5	44.0-60.0	50.5	6.9	36.0-50.0	44.1	7.5	**
F6	42.6-54.0	48.7	5.5	35.4-52.0	43.5	8.9	**
			Grain protein content (%)				
F4	9.2-13.8	11.1	7.6	9.0-11.8	10.1	6.0	**
F5	12.4-14.3	13.3	3.4	11.8-13.7	12.9	3.4	**
F6	11.9-16.0	14.4	7.4	12.2-16.0	14.1	4.6	ns
			Wet gluten content (%)				
F4	21.2-44.3	27.5	15.1	19.2-31.6	24.1	14.3	**
F5	30.7-47.7	38.8	10.2	25.6-42.6	33.0	12.7	**
F6	24.2-47.0	34.9	12.9	23.9-38.0	31.9	9.7	**
			Gluten index (%)				
F4	50.0-99.0	89.6	12.5	28.9-99.5	84.4	21.0	ns
F5	32.0-96.0	66.8	26.1	44.9-98.3	80.4	20.8	**
F6	28.8-97.0	69.1	24.7	13.8-98.0	73.6	28.3	**
			Zeleny sedimentation value (ml)				
F4	26.5-59.5	42.1	21.9	19.0-44.0	30.1	19	**
F5	43.5-67.5	57.6	9.6	33.0-60.0	45.4	15.1	**
F6	33.5-69.0	57.8	17.3	34.0-65.0	46.6	17.7	**
			Pelshenke value (min)				
F4	27.0-96.5	61.7	28.8	25.5-104.0	55.0	33.5	ns
F5	30.0-140.5	78.8	36.4	32.0-122.0	69.8	31.2	ns
F6	55.5-197.0	126.6	29.9	66.5-176.0	116.5	27.1	*

Range (minimum-maximum), CV (%) - coefficient of variation

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Table 2. Realized heritability between segregating generations F4/F5 and F5/F6 for six traits in the crosses Golubica × Emesse (G×E) and Verbunkos × Soissons (V×S)

Heritability estimator	G×E		V×S	
	F4/F5	F5/F6	F4/F5	F5/F6
	1000 kernel weight (g)			
h^2_b	0.60 **	0.53 **	0.69 **	0.64 **
$h^2_{high-low}$	0.71	0.41	0.72	0.63
$h^2_{high-average}$	0.74	0.35	0.54	0.50
$h^2_{average-low}$	0.69	0.49	0.87	0.75
	Grain protein content (%)			
h^2_b	0.40 **	0.21 ns	0.35 **	0.30 *
$h^2_{high-low}$	0.50	0.12	0.39	0.37
$h^2_{high-average}$	0.53	0.20	0.47	0.38
$h^2_{average-low}$	0.46	0.04	0.30	0.35
	Wet gluten content (%)			
h^2_b	0.54 **	0.43 **	0.69 **	0.62 **
$h^2_{high-low}$	0.55	0.41	0.65	0.57
$h^2_{high-average}$	0.54	0.44	0.64	0.51
$h^2_{average-low}$	0.56	0.37	0.66	0.64
	Gluten index (%)			
h^2_b	0.60 **	0.55 **	0.76 **	0.59 **
$h^2_{high-low}$	0.80	0.50	0.73	0.65
$h^2_{high-average}$	1.35	0.39	0.98	0.71
$h^2_{average-low}$	0.56	0.61	0.60	0.61
	Zeleny sedimentation value (ml)			
h^2_b	0.32 *	0.49 **	0.37 **	0.48 **
$h^2_{high-low}$	0.31	0.41	0.38	0.46
$h^2_{high-average}$	0.05	0.53	0.28	0.41
$h^2_{average-low}$	0.63	0.29	0.50	0.50
	Pelshenke value (min)			
h^2_b	0.69 **	0.79 **	0.43 **	0.53 **
$h^2_{high-low}$	0.78	0.80	0.33	0.45
$h^2_{high-average}$	0.76	0.67	0.53	0.52
$h^2_{average-low}$	0.79	0.94	0.09	0.36

* and ** significant at P<0.05 and P<0.01, respectively; ns-not significant

Table 3. Correlations among different estimators of realized heritability calculated between segregating generations F4/F5 and F5/F6 of the crosses Golubica × Emesse (G×E) and Verbunkos × Soissons (V×S)

Heritability estimator	F4/F5			F5/F6		
	$h^2_{high-low}$	$h^2_{high-average}$	$h^2_{average-low}$	$h^2_{high-low}$	$h^2_{high-average}$	$h^2_{average-low}$
			G×E			
h^2_b	0.94 **	0.72	0.56	0.98 **	0.86 *	0.96 **
$h^2_{high-low}$		0.89 *	0.36		0.89 *	0.97 **
$h^2_{high-average}$			-0.03			0.75
			V×S			
h^2_b	0.96 **	0.79	0.73	0.87 *	0.63	0.81 *
$h^2_{high-low}$		0.70	0.86 *		0.77	0.91 *
$h^2_{high-average}$			0.25			0.42

* and ** significant at P<0.05 and P<0.01, respectively

downward screening for one population and upward screening for the other population. In the present study protein content showed higher heritability estimates for upward ($h^2_{high-average}$) than for downward screening ($h^2_{average-low}$), which is in agreement with results of Nishio et al. (2005). For other traits in our study heritability estimates based on upward and downward screening varied between two crosses but also between generations within the cross G×E (Table 2).

Correlations among traits

In the present study 1000 kernel weight was in a positive correlation with several quality traits, but results were inconsistent across generations and crosses (Table 4). In the F4 and F5 generations for the cross V×S 1000 kernel weight was in positive correlation with protein content (0.46 and 0.60). Nishio et al. (2005) also reported positive correlations between 1000 kernel weight and protein content in F3 and F4 generations of two wheat crosses, but with considerably lower values (0.202 to 0.244). In

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Table 4. Correlations among traits in F4, F5 and F6 generations of the crosses Golubica × Emesse (G×E) and Verbunkos × Soissons (V×S)

Trait		GPC (%)	WGC (%)	GI (%)	ZSV (ml)	PV (min)
			F4 generation			
TKW (g)	G×E	-0.22	-0.23	0.21	-0.20	-0.09
	V×S	0.46 **	0.36 **	-0.24	0.35 **	0.32 *
GPC (%)	G×E		0.80 **	-0.62 **	0.73 **	0.05
	V×S		0.68 **	-0.36 **	0.61 **	0.26
WGC (%)	G×E			-0.86 **	0.70 **	-0.19
	V×S			-0.68 **	0.62 **	0.04
GI (%)	G×E				-0.47 **	0.47 **
	V×S				-0.14	0.17
ZSV (ml)	G×E					0.06
	V×S					0.36 **
			F5 generation			
TKW (g)	G×E	-0.20	-0.23	0.22	-0.17	-0.07
	V×S	0.60 **	0.50 **	-0.39 **	0.11	0.02
GPC (%)	G×E		0.83 **	-0.61 **	0.20	-0.15
	V×S		0.76 **	-0.57 **	0.07	-0.19
WGC (%)	G×E			-0.76 **	0.15	-0.37 **
	V×S			-0.80 **	0.10	-0.39 **
GI (%)	G×E				0.13	0.58 **
	V×S				0.15	0.52 **
ZSV (ml)	G×E					0.23
	V×S					0.19
			F6 generation			
TKW (g)	G×E	-0.20	-0.30 **	0.13	-0.15	0.01
	V×S	0.13	0.14	-0.10	0.14	0.32 *
GPC (%)	G×E		0.80 **	-0.29 *	0.81 **	0.49 **
	V×S		0.55 **	-0.21	0.55 **	-0.18
WGC (%)	G×E			-0.62 **	0.70 **	0.07
	V×S			-0.64 **	0.38 **	-0.51 **
GI (%)	G×E				-0.16	0.37 **
	V×S				0.23	0.47 **
ZSV (ml)	G×E					0.48 **
	V×S					-0.01

* and ** significant at P<0.05 and P<0.01, respectively; TKW - 1000 kernel weight; GPC - grain protein content; WGC - wet gluten content; GI - gluten index; ZSV - Zeleny sedimentation value; PV - Pelshenke value

the present study correlation between 1000 kernel weight and wet gluten content was positive in F4 and F5 generations of the cross V×S (0.36 and 0.50) and negative in F6 generations of the cross G×E (-0.30). For the cross V×S 1000 kernel weight was also in a positive correlation with Zeleny sedimentation value in the F4 generation (0.35) and with Pelshenke value in F4 and F6 generations (0.32), while in negative correlations with gluten index in the F5 generation (-0.39).

For both crosses in F4 and F6 generations significant positive correlations among protein content, wet gluten content and sedimentation value were determined, while in the F5 generation a significant positive correlation was determined between protein content and wet gluten content only (Table 4). A considerably higher values of correlation coefficients between these traits were determined for the cross G×E (0.70 to 0.83) than for V×S (0.38 to 0.74). This is in agreement with previous reports on the correlations of protein content with wet gluten content of 0.71 (Fossati et al., 2010) and 0.85 (Gröger et al., 1997), grain protein content with Zeleny sedimentation value of 0.78 (Gröger et al., 1997), 0.44 (Fossati et al., 2010), 0.52 (Zeleny et al., 1960) and 0.72 (Branlard et al., 1992) as well as between wet gluten content and sedimentation value of 0.71 (Fossati et al., 2010).

In the present study gluten index was in all generations of both crosses in negative correlation with wet gluten content (-0.86 to -0.62) and in moderate positive correlation with Pelshenke value (0.37 to 0.58). The Pelshenke value was in positive correlations with Zeleny sedimentation value in the F4 generation for the cross V×S (0.36), and in F6 generation for the cross G×E (0.48) as well as with protein content in F6 generation of the cross V×S (0.49). Fisher et al. (1989) also reported moderate positive correlations of 0.31 and 0.42 between protein content and Pelshenke value in F3 and F7 generations of a wheat cross.

Conclusion

Realized heritability of indirect quality traits, estimated as parent-offspring regression (h^2_b), ranged from 0.21 to 0.79. Realized heritability averaged over crosses (G×E and V×S) and generations (F4/F5 and F5/F6) was much higher for wet gluten content, gluten index and Pelshenke value than for other quality traits suggesting the suitability of these traits as good selection criteria for improvement of bread-making quality. Correlations among the four methods used to calculate realized heritability revealed the best agreement between h^2_b and $h^2_{high-low}$ and the lowest between $h^2_{high-average}$ and $h^2_{average-low}$ heritability

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estimators. Furthermore, a strong positive correlation observed among grain protein content, wet gluten content and Zeleny sedimentation value as well as strong negative correlations of gluten index with grain protein content and wet gluten content have both to be considered when selecting for superior bread-making quality.

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