Plant Breeding **120**, 13—19 (2001)

ISSN 0179-9541

Genetic analysis of bread-making quality in wheat and spelt

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With 1 figure and 2 tables

Received January 5, 2000/Accepted July 25, 2000
Communicated by C. Lorenzoni

Abstract

Bread-making quality in wheat and spelt reflects the combination of several, mostly quantitatively inherited parameters. The aim was to find molecular markers linked to quantitative trait loci (QTL) for quality parameters. Zeleny sedimentation values (Zel), protein (Prot), kernel hardness (KH) and 1000-kernel weight (TKW) of 226 F_5 recombinant inbred lines (RILs) from a cross between wheat and spelt were assessed in different environments. The dough properties of 204 RILs were assessed with an alveograph. Based on a genetic map of 187 loci, nine QTL were found for Zel and Prot, explaining 47% and 51% of the phenotypic variance, respectively. Fifty-four per cent of the variance was explained by 10 QTL for KH and eight for TKW. For the alveograph parameters 10 QTL were found for baking strength, nine for tenacity, seven for configuration ratio, and four for elasticity index and extensibility. The phenotypic variance explained ranged from 25% to 48%. The population mean of the dough parameters was shifted towards the spelt parent. It is concluded that non-additive effects are crucial in the expression of high bread-making quality of wheat. The consequences for wheat and spelt breeding programmes are discussed.

Key words: *Triticum aestivum* — *Triticum spelta* — alveograph — bread-making quality — QTL

Quality parameters, as with many economically relevant traits are characterized by a continuous distribution, which suggests that they are influenced by several genes. Quantitative trait loci (QTL) analysis allows quantitatively inherited traits to be resolved into their individual genetic components. The number of QTL studies is still limited for hexaploid wheats because of the complexity of its genome. Studies published to date have focused on QTL for pathogen resistance (Faris et al. 1997, Nelson et al. 1997, 1998, Keller et al. 1999b, Messmer et al. 2000), lodging resistance (Keller et al. 1999a) and preharvest sprouting resistance (Anderson et al. 1993, Zanetti et al. 2000). Only a few studies have investigated QTL for quality parameters in hexaploid (Sourdille et al. 1996) or tetraploid wheat (Blanco et al. 1996, 1998).

Spelt is an interesting (hexaploid) crop for marginal regions where environmental factors prevent the cultivation of wheat. Compared with wheat, spelt is taller (150–200 cm), has long, lax ears (15–20 cm), a brittle rachis and tight glumes (Winzeler et al. 1994). Since spelt possesses a unique flavour, a higher vitamin content and is more nutritious than wheat (Campbell 1997), the demand for products made exclusively of spelt has increased. In order to support the spelt production a breeding programme was established at the Swiss Federal Research Station for Agroecology and Agriculture (Zurich, Switzerland) in 1979 (Winzeler and Rüegger 1990). For the improvement of yield and resistance to lodging and disease in spelt, wheat varieties were used as crossing partners.

In order to gather information about the inheritance of quality parameters and dough characteristics in hexaploid cereals, 226 F_5 recombinant inbred lines (RILs) of a wheat × spelt cross were used. This cross was carried out because of the reported higher degree of polymorphism between wheat and spelt than within wheat (Siedler et al. 1994) and the strong difference between wheat and spelt in their rheological characteristics (Ranhotra et al. 1995). The aim of this study was: (1) to clarify the difference between hexaploid wheat and spelt in their bread-making quality; (2) to resolve the quantitatively inherited quality parameters and dough properties into their individual genetic components; and (3) to study any gene interactions. The results will contribute to a better understanding of the inheritance of complex quality traits and to more efficient strategies in wheat and spelt breeding programmes.

Materials and Methods

Plant materials and phenotypic data assessment: The investigated plant population consisted of 226 F_5 RILs derived from the cross between the Swiss winter wheat (*Triticum aestivum* L.) variety 'Forno' and the Swiss winter spelt (*Triticum spelta* L.) variety 'Oberkulmer'. The four experimental field trials consisted of 250 entries (226 RILs, the parental lines with three replicated entries each, 11 spelt and seven wheat varieties) arranged according to an α-lattice design with two replications, comprising 50 incomplete blocks with 10 genotypes each. The field trials were located in 1996 at the Swiss Federal Research Station for Agroecology and Agriculture (Fal96) and at Eschikon (Esc96), in 1997 at Rossberg (Ros97) and in 1998 at Oensingen (Oen98). For more details see Zanetti et al. (2000).

The crop was harvested by a combine, and afterwards dehulled (Mühlenbau, Bad Friedrichshall-Kochendorf, Germany). The 1000-kernel weight (TKW) was assessed for each entry from the three environments Fal96, Ros97 and Oens98. A kernel sample ($\approx$ 50 g) of each entry of all four environments was processed to flour (Brabender mill, OHG, Duisburg, Germany), which was used to measure protein content (Prot) and kernel hardness (KH) by near infrared reflectance (Inframatic 8611, PerCon, Perten Instruments, Huddinge, Sweden) and for determination of Zeleny sedimentation value (Zel) (ICC 1996).

A larger quantity of flour (500 g) was needed for rheological measurements. Thus, an automatic mill (Bühler, Uzwil, Switzerland) was used to grind the remaining kernels of the two replicates of six wheat and nine spelt standards, as well as the parental varieties from three

environments (Fal96, Esc96 and Ros97). The two replications of 204 RILs harvested in Ros97 were pooled and this pooled material was ground to flour using the same mill. An alveograph (Alvéograph NG, Chopin, tripette & renaud, Villeneuve-la-Garenne, France) was used for rheological measurements, which is a technique based on subjecting dough to biaxial extension until it ruptures (Chopin 1927). Alveograms were processed for the pooled material of the 204 RILs from Ros97, and all entries of parental lines and standards from the environments Fal96, Esc96 and Ros97. Using the standard procedure for the alveographic measurements, tenacity (P in mmH_2O), extensibility (L in mm), baking strength (W in 10^{-4} J), configuration ratio of the curve (P:L) and elasticity index (Ie in percentage) were assessed.

Statistical analysis: Using the computer program PLABSTAT (Utz 1995) lattice analysis of single environments and ANOVA were performed over four environments for Zel, Prot, KH, and over three environments for TKW. The adjusted entry means (i.e. mean values of the genotypes adjusted for block effects) and effective error mean squares obtained from the lattice analysis were used for a combined ANOVA over environments in order to estimate the genotypic (σ^2_g), the environmental (σ^2_e) as well as the genotype × environment interaction (σ^2_{ge}) variance components. On the basis of the variance components of the ANOVA the heritability (h^2) of the traits was estimated according to the formula

$$h^2 = \sigma^2_g/\{\sigma^2_g + (\sigma^2_{ge}/E) + (\sigma^2_{error}/(E \times R))\}$$

E and R are the number of environments and replicates, respectively (Hallauer and Miranda Fo 1981). For the alveographic parameters, the ANOVA was performed exclusively with the values of the wheat and spelt standards including the parental lines and the respective variance components were used for estimating h^2. Using SAS (SAS Institute 1988) the phenotypic data were tested for their normal distribution by the Shapiro–Wilk statistic. Pearson and Spearman rank correlation coefficients and multiple regressions between phenotypic data were also calculated over all environments as well as in single environments.

QTL analysis: In order to saturate the genetic map published by Messmer et al. (1999) for the chromosome groups 1 and 6, 10 additional restriction fragment length polymorphism (RFLP) markers were tested for polymorphism between the parental varieties and a clone (pUTVAy) containing the entire coding region of Ay high molecular weight (HMW) glutenin gene from *Triticum urartu* (R. D'Ovidio, pers. comm.). Polymorphic markers (pUTVAy, BCD0508, BCD0808 and KSUD027) were tested on the RILs. Moreover, the RILs were analysed by gel electrophoresis for the banding pattern of seed storage proteins by the group of Prof. C.-U. Hesemann (University of Hohenheim, Germany) according to the methods described by Radic et al. (1997) and Radic-Miehle et al. (1998). The data for additional RFLP markers and the protein data were integrated into the genetic map, as described by Messmer et al. (1999). The map used for the QTL analysis consisted of 187 loci with 24 linkage groups and spanned a distance of 2679 cM, corresponding to approximately two-thirds of the wheat genome. QTL analysis was performed for each location and over environments by the software package PLABQTL (Utz and Melchinger 1996). The computation was based on composite interval mapping and was carried out with the data set of 204 genotypes (excluding genotypes with more than 10% of the markers being heterozygous). Cofactors were determined by the procedure cov SELECT. The threshold for the detection of the QTL was fixed at a LOD (log of the odds) value of 3.0. The phenotypic variance explained by all QTL together and by a single quantitative trait locus was calculated. In addition to the additive model, a model was run for the detection of epistatic effects between QTL.

Results

Genetic map

The data for the markers investigated and of the protein banding patterns were integrated into the genetic map (Messmer et al. 1999). BCD0808 and KSUD027 were assigned to 4A and 6AL, respectively. However, they were closely linked to other markers and did not improve the size of the genetic map. BCD0508 was assigned to 1BL (Fig. 1), although the distance to the closest marker was too large to be significantly linked. The clone pUTVAy revealed two polymorphic loci. One locus (*pUTVAyb*) mapped to the 1BL, whereas the locus *pUTVAya* was closely linked with three RFLP markers that were assigned to 5AS by Messmer et al. (1999). Since locus *pUTVAya* is expected to be located on chromosome group 1 these markers were assigned to a new linkage group ('1AL_5AS'). Three different protein alleles could also be mapped. The LMW glutenin 'Prot_low' ('Forno' band (F), 42.8 kDa; 'Oberkulmer' bands (O), 44.0 and 47.8 kDa) was mapped to 1BS 5 cM away from R1F2, a wheat microsatellite within the coding region of a γ-gliadin pseudo gene (Devos et al. 1995). The HMW glutenin 'Prot_A1' (F, none; O, 109.9 kDa) was closely linked to *pUTVAya* (linkage group '1AL_5AS'), whereas HMW glutenin 'Prot_D1' (F: 80.1 kDa, O: 76.4 kDa) was assigned to 1DL. The size of the map was increased from 2469 cM (Messmer et al. 1999) to 2679 cM.

Phenotypic variation for Zel, Prot, KH and TKW

Across four environments 'Oberkulmer' had a significantly lower Zel but a significantly higher Prot than 'Forno'. The parental lines had similar KH and TKW values (Table 1). The population showed a pronounced positive and negative transgressive segregation for all four traits. The phenotypic data were significantly ($P < 0.01$) correlated between environments. The correlation coefficient between environments ranged from 0.75 to 0.86 for Zel, from 0.79 to 0.87 for Prot, from 0.72 to 0.79 for KH and from 0.43 to 0.70 for TKW. Components of variance obtained by the ANOVA were all highly significant among RILs ($P < 0.01$) for all traits. The genotypic variance component had the strongest effect on the phenotypic variance of Zel, Prot and KH, whereas the phenotypic variance of TKW was influenced the most by the environment. The heritability values ranged between 0.96 for Prot and 0.87 for TKW. The traits Prot and KH were strongly correlated ($r = -0.93$), whereas both traits were moderately correlated with Zel ($r = 0.39$ for Prot; $r = -0.39$ for KH; $P < 0.01$). Other correlation combinations between Zel, Prot, KH and TKW were not significant.

Phenotypic variation for dough properties

Averaged across three environments the parental lines differed significantly from each other for alveographic parameters (Table 1). Whereas 'Forno' was characterized by a strong dough, reflected in a high P and rather low L value, 'Oberkulmer' had a weak, extensible dough (low P and high L value). Comparing the parental lines with the wheat and spelt standards, it became evident that the parental lines represent the typical dough properties of the respective species. For the standards and the parental lines, all alveographic parameters were highly significantly ($P < 0.01$) correlated between replications ($0.77 \le r \ge 0.98$) as well as between the three environments tested ($0.81 \le r \ge 0.98$). Based on the components of variance of

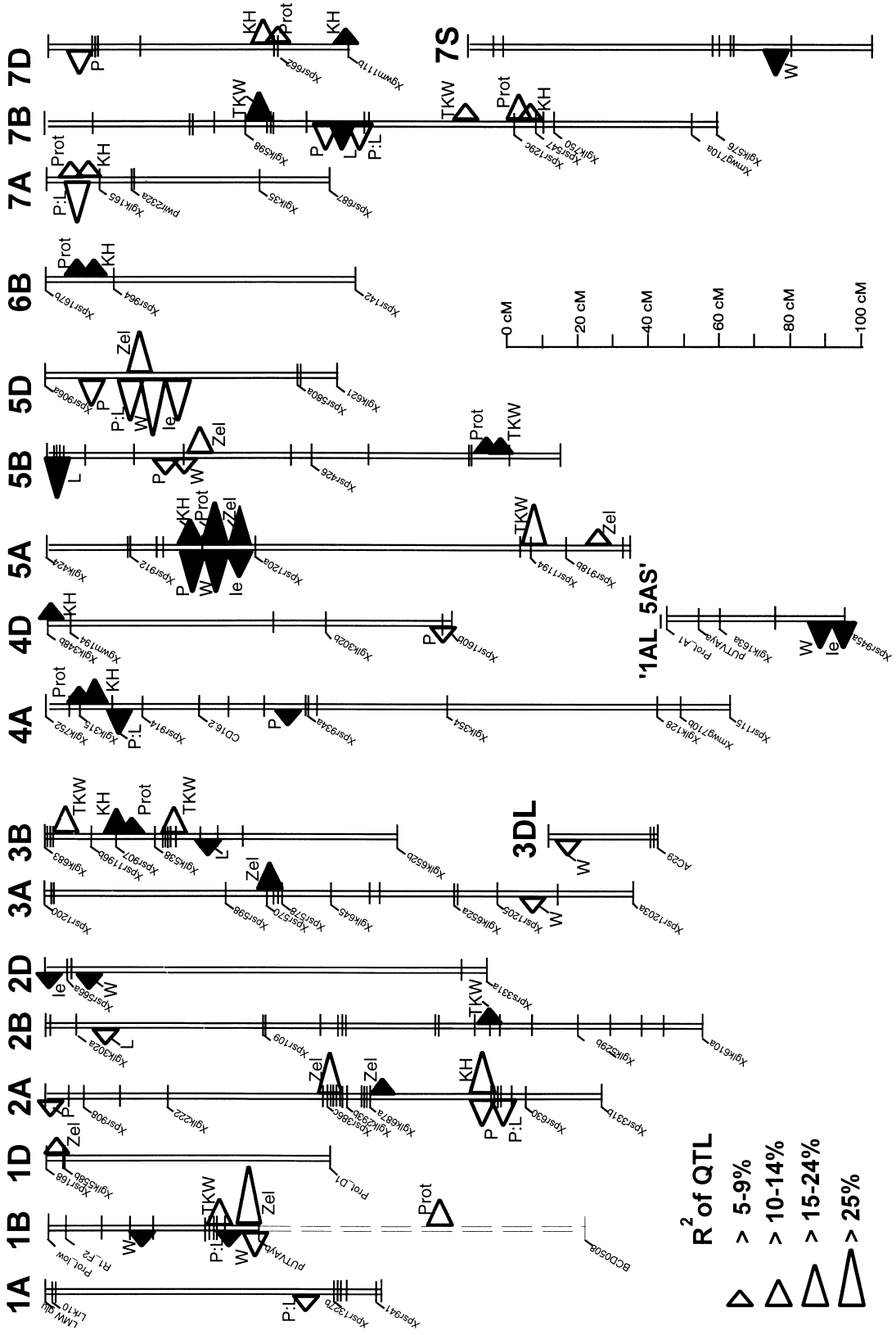

Fig. 1: Location of significant (LOD > 3.0) for quantitative trait loci (QTL) for indirect quality parameters and for dough properties: Zeleny sedimentation values (Zel), protein content (Prot), kernel hardness (KH), 1000-kernel weight (TKW), tenacity (P), extensibility (L), baking strength (W), elasticity index (Ie) and configuration ratio (P:L) on the genetic map of 204 recombinant inbred lines derived from the cross 'Forno' × 'Oberkulmer'. Filled, open triangles indicate that the positive allele was inherited from 'Oberkulmer' and 'Forno', respectively. The triangle size reflects the phenotypic variance (R^2) explained by a single QTL

Table 1: Mean and range of indirect quality parameters (Zeleny sedimentation value (Zel), protein content (Prot), kernel hardness (KH), 1000-kernel weight (TKW)) and alveographic parameters (tenacity (P), extensibility (L), baking strength (W), configuration ratio (P:L), elasticity index (Ie)) of wheat and spelt standards, parental varieties and F_5 recombinant inbred lines (RILs) of the cross 'Forno' × 'Oberkulmer' across environments. The alveographic parameters of the RILs were assessed only in the environment Ros97

	Indirect quality parameters[1]				Alveographic parameters[2]				
	Zel (ml)	Prot (%)	KH (%)	TKW (g)	P (mmH_2O)	L (mm)	W (10^{-4} J)	P:L	Ie (%)
Standard cultivars									
Wheat									
Mean	52.8	13.3	22.5	46.2	152	69	358	2.81	58
Range	25–67	10.4–14.8	20.3–26.2	42.4–48.7	134–206	51–90	283–417	1.91–3.24	49–67
Spelt									
Mean	30.9	13.3	22.9	46.4	45	176	146	0.28	38
Range	18–38	12.6–16.6	19.4–24.8	40.0–55.2	39–53	148–207	106–178	0.22–0.36	31–42
Parental lines									
'Forno'									
Mean	52.9	12.8	22.0	51.2	157	51	286	3.63	50
Range	52–55	12.6–12.9	21.8–22.5	51.0–51.5	156–158	48–54	267–301	3.44–4.00	49–52
'Oberkulmer'									
Mean	33.1	14.8	22.0	53.9	50	185	158	0.30	36
Range	32–34	14.6–15.1	21.8–22.3	53.1–54.6	48–54	174–194	147–175	0.28–0.33	35–39
Population									
RILs									
Mean	38.9	13.9	22.6	51.0	61	193	194	0.35	36
Range	22–60	10–20	15–28	42–59	27–116	81–295	80–365	0.10–0.93	23–52
LSD[3]	5.7	1.0	1.6	4.3	18	36	65	1.25	6

[1] Zel, Prot and KH were assessed in four environments and TKW in three.
[2] Alveographic parameters were assessed in three environments for all standard cultivars and the parental lines, and in one environment for RILs.
[3] Least significant difference ($P < 0.05$) obtained of the ANOVA performed over environments.

the ANOVA of the standards and the parental lines, the heritability values were above 0.90.

In the same segregating population, alveographic data were assessed considering 204 RILs (excluding the 22 RILs with more than 10% heterozygous markers) grown in Ros97. The population mean was significantly ($P < 0.01$) different from the parental mean (Table 1) for all dough parameters except for the W value. In general, the population means were shifted towards the spelt parent. For P, L and P:L, the population showed transgression to one side only, and none of the RILs reached values similar to those of 'Forno'. For Ie, a few RILs just reached the value of 'Forno'. For W significant transgression was observed on both sides.

Correlations among alveographic parameters were highly significant ($P < 0.01$) except for those between L and W as well as for L and Ie. Correlation coefficients between alveographic parameters and Zel, Prot, KH or TKW are listed in Table 2. Zel showed the highest correlation with W, Ie, and P. Prot had the strongest correlation with P, whereas KH was the most negatively correlated with P, and to P:L. TKW showed no significant correlation with alveographic parameters.

QTL for Zel, Prot, KH and TKW

Based on means over four environments, nine QTL were found for each of Zel and Prot, 10 for KH and eight for TKW (Fig. 1). All QTL together explained 47% of the phenotypic variance of Zel, 51% of Prot, 54% of KH and 54% of TKW. For all traits, both parental varieties contributed positive alleles. 'Forno' contributed at six chromosomal regions to a higher Zel, at four regions to a higher Prot and a lower KH, and at five regions to a higher TKW.

Of the nine QTL involved in the phenotypic expression of Zel, four had a major effect ($R^2 > 15\%$). These were located on 1B, 2A (80 cM), 5A (50 cM) and 5D. The QTL on 1B was linked to the marker pUTVAy. Where the allele of 'Forno' contributed to an increase in Zel, this QTL was detected in each environment. The additive effects in the single environments ranged from 2.4 ml in Fal96 and Oen98 to 4.5 ml in Ros97. In addition, the QTL on 5A, where the allele of spelt parent increased Zel, was also confirmed in all environments. The additive effects varied between 2.5 ml in Oen98 and 3.9 ml in Esc96. For Prot, the QTL on 5A was the only one with a major effect ($R^2 > 15\%$) and was confirmed in all environments. Of nine QTL for Prot seven coincided with QTL for KH. The only QTL with a major effect on KH (on 2A) did not coincide with a QTL for Prot. The phenotypic expression of TKW was mostly influenced by the QTL on 5A ($R^2 = 23\%$).

QTL for parameters of dough properties assessed in Ros97

Ten QTL were involved in the phenotypic expression of W, explaining 39% of its variance (Fig. 1). For P, nine QTL explained 48% of its variance and for P:L seven QTL explained 38% of its variance. Four QTL were found for L and Ie, explaining 25% and 30% of the phenotypic variance, respectively. 'Forno' contributed the allele for higher L and Ie values at one chromosomal region, at five genome regions to enhanced W and P:L-values, and at seven regions to higher P-values. QTL with major effects ($R^2 > 15\%$) were detected for P and W on 5A, for L on 5B, and for W, P:L and Ie on 5D. The four QTL detected for Ie coincided with QTL for W. Three coinciding QTL (on 5A, 5B and 5D) were found for W and P. On 7B, coinciding QTL were detected for P, L and P:L.

Table 2: Correlation coefficients between alveographic parameters (P, L, W, P:L and Ie), Zeleny value (Zel), protein content (Prot), kernel hardness (KH) and 1000-kernel weight (TKW) investigated with recombinant inbred lines (RILs) from the 'Forno' × 'Oberkulmer' cross in the environment Ros97

	P (mmH_2O)	L (mm)	W (10^{-4} J)	P:L	Ie (%)
L (mm)	−0.47***				
W (10^{-4} J)	0.78***	0.01			
P:L	0.79***	−0.83***	0.37***		
Ie (%)	0.50***	−0.14	0.80***	0.32***	
Zel[1] (ml)	0.63**	0.06	0.87**	0.27**	0.73**
Prot[1] (%)	0.43***	−0.06	0.25**	0.27**	−0.01
KH[1] (%)	−0.55***	0.21**	−0.28**	−0.43***	0.02
TKW[1] (g)	−0.03	0.04	−0.04	−0.05	−0.05

,* Significant at P = 0.05 and P = 0.01, respectively.
[1] The correlation values of other parameter combinations are indicated in the text.

QTL for Zel coincided at four locations on 1B, 5A, 5B and 5D with QTL for W. QTL for Zel coincided at three and two further genome regions with P and Ie, respectively. Of the three coincidences found between QTL for KH and for P:L, two also coincided with QTL for Prot (4A and 7A).

Epistatic effects between QTL of the parameters investigated

Digenic epistatic effects were tested for all parameters. Of six significant QTL × QTL interactions, three had a strong effect: for Prot the QTL on 3B and 7D, for P:L the QTL on 1A and 5D and for Ie those on 2D and 5D. In the multiple regression, the gene interactions of Prot, Ie and P:L had a part R^2 of 8.8%, 2.9% and 4.0%, respectively. The two interfering QTL of Prot and Ie inherited the positive allele of 'Oberkulmer' at one locus and the allele of 'Forno' at the other.

Discussion

Genetic basis of indirect quality parameters of wheat and spelt

The high heritability values of Zel, Prot, and KH ($h^2 \geq 0.95$) demonstrated that it is possible to select effectively for these traits in a breeding programme. A pronounced segregation and continuous variation were observed for Zel, Prot, KH and TKW. This suggests that several genes with major or minor effects are involved in the phenotypic expression of these traits. Indeed, the number of QTL detected was between eight for TKW and 10 for KH. Sourdille et al. (1996) reported five genomic regions to be involved in KH in wheat. Prot was controlled by six QTL in durum wheat (Blanco et al. 1996). In contrast, Matuz (1998) estimated by generation-mean analysis that only one gene caused the difference between the parental lines for sedimentation volume of two wheat crosses. Reasons for a lower number of genes detected or estimated might include the genetic background, the population size, the number of environments and/or the marker coverage.

In this study, the effects of most QTL were relatively small. One region strongly affecting Zel ($R^2 > 15\%$) was linked to the marker for HMW glutenin (*pUTVAyb*) located on 1B. HMW glutenin is considered to be a crucial factor for bread-making quality as well as LMW glutenins and gliadins (Shewry et al. 1995). Thus, one might expect to find QTL at the sites known to encode for HMW and LMW glutenin (located on the long and short arm of the chromosome group 1) as well as for gliadins controlled by two complex loci on homoeologous chromosomes of group 1 and 6. In the population studied, only HMW glutenin on 1BL appeared to have a significant effect on quality, even though the parental lines also differed in the HMW ('1AL_5AS', 1 DL) and LMW (1AS, 1BS) glutenins. It is possible that the effects of genes encoding gliadins on chromosome group six might remain undetected because of the low marker coverage.

Snape et al. (1995) argued that the chromosomes of homoeologous group 5 were major determinants for the differences in Prot with the strongest effect on 5D. Indeed, in this study, Prot was strongly affected by a genomic region on 5A. Moreover, all three chromosomes of group 5 had a genomic region influencing Zel, reflecting gluten quality and quantity with the strongest effect on 5A. The strong negative correlation between Prot and KH was confirmed by a high degree of coinciding QTL. Thus, these traits are predominately controlled by similar genomic regions.

Complex inheritance of dough properties

Despite the different growing and harvesting conditions, the dough parameters of the wheat and spelt standard lines were highly significantly correlated between the different environments resulting in high heritability values ($h^2 \geq 0.90$). This is in line with the results of Robert and Denis (1996) reporting that the genetic component represented the largest amount of total variation. The number of QTL for the different dough parameters ranged from four (L and Ie) to 10 (W). The high complexity of dough properties might contribute to the generally lower percentage of variance explained. Dough parameters are influenced by several partly unknown features and might be controlled by a larger number of genes compared with the indirect parameters. Therefore, their effects might be below the detection limit of our population. In addition, the traits involved in rheological properties might counteract each other, as discussed below.

Both parental lines contributed positive alleles to all the traits investigated. Despite this fact, the dough parameters showed transgression only to one side and the population mean was shifted towards 'Oberkulmer'. This is an indication for the involvement of non-additive gene effects. Indeed, six significant epistatic effects were found. Since only digenic epistatic effects between genomic regions with significant additive effects were tested, additional interactions might be undetected but be important for the dough parameters. Lefebvre and Palloix (1996) tested all marker combinations for digenic epistatic effects with relevance for *Phytophthora* resistance in pepper. As

a result, some interactions were detected between genomic regions without any additive effects, suggesting that some genes may be effective only in the presence of other genes.

In addition to the interaction between genes the interaction between traits might also be important for dough characteristics. By means of multiple regression (data not shown) all indirect parameters (Zel, Prot, KH, TKW) entered the models, even though some parameters were highly correlated and together explained 28%, 43% and 65% of the variance of L, P:L and P, respectively. Interaction between traits was also reported by Branlard (1998) who outlined that certain allele combinations of HMW glutenin at the *Glu-D1* locus only have a positive effect if Prot is higher than 13.5%. This result illustrates that both the optimal interaction between different traits and the optimal gene interaction are important for dough parameters. The wheat parent 'Forno' does not represent a high accumulation of alleles with maximal effects but a good combination of genes for various parameters required for bread-making of wheat. Thus, the probability of finding a RIL with improved dough characteristic compared with the wheat parent is low. Therefore, it is not surprising that we could not detect any positive transgression for the dough properties P, L and P:L in our wheat × spelt population. Schmid et al. (1994) tested wheat × spelt F_1 hybrids for Prot and Zel and found negative heterosis effects. This is a further indication of the importance of an optimal combination of both genes and traits to reach the baking quality required for wheat.

Would indirect selection for dough properties be a satisfying strategy?

In this population, Zel was highly correlated with P, W and Ie. The parameters L and P:L were reflected best by the trait KH. The relationship between Zel and dough properties was confirmed by coinciding QTL for Zel and W at four regions (1B, 5A, 5B, 5D); three were found to be involved in the phenotypic expression of P (5A, 5B and 5D). The strong effect of the QTL on 5A and 5D might have contributed to the high phenotypic correlation. The correlation between KH and P:L was confirmed by three coinciding QTL (2A, 4A and 7A). While for Zel, Prot and KH, transgression was present towards both sides exclusively negative transgression for P, L and P:L was detected. Therefore, the high correlation between dough parameters and Zel or KH are insufficient to guarantee a satisfactory improvement of the dough properties by indirectly selecting for Zel and KH. This might be attributed to the fact that QTL were found which were involved exclusively in the dough properties, Zel or KH. Alternatively, this could be due to the strong influence of the non-additive effects mentioned above. Consequently, we can conclude that the success of improving dough properties by selecting for Zel and KH is limited. Thus, this highlights the need to directly assess dough properties at least in advanced plant material.

Consequences for spelt and wheat breeding programmes

For spelt breeding, these results suggest that the apprehension of losing the typical dough characteristic of spelt by the introgression of wheat is not justified. Thus, wheat could be used as a source for lodging and disease resistance, as proposed by Campbell (1997), without losing the typical dough characteristics of spelt.

Spelt yield cannot be increased by an enhanced spikelet density or kernel number per spikelet without losing its typical ear morphology. Thus, TKW is an important yield component to select for. Although the parental lines did not differ significantly for TKW the maximal TKW found among RILs was 59 g. Since TKW was not correlated with any of the quality and dough parameters, it is possible to select for TKW without changing the dough characteristics. Moreover, none of the QTL for quality parameters coincided with the *q*-locus located on 5AL responsible for the typical ear morphology of spelt and indirectly for preharvest sprouting resistance (Zanetti et al. 2000).

For wheat breeding, one can conclude that, with respect to quality, no improvement or maintenance can be achieved with wheat × spelt RILs. It is not possible to transfer the high Prot from spelt into wheat without affecting the dough properties typical for wheat. The three QTL for Prot where the positive allele came from the spelt parent, and which did not coincide with QTL for dough parameters (3B, 5B and 6B), had small effects. In addition, the significant epistatic effect between the QTL for Prot on 3B and 5B would hamper the use of these chromosomal regions. Because of the significant non-additive effects it might be advantageous for improving the bread-making quality of wheat to cross genetically narrow elite lines in order to conserve optimal trait and gene combinations. This might be one reason for the high degree of genetic similarity between wheat varieties detected at the molecular level by Siedler et al. (1994). Therefore, the efforts to maximize several indirect parameters by conventional selection in early generations or to combine QTL with significant additive effects by marker-assisted selection will have limited success in improving dough parameters and thus rheological tests cannot be replaced. However, when transferring traits other than quality from spelt to wheat, marker-assisted backcross breeding can be used in order to conserve the chromosomal regions responsible for wheat quality.

Acknowledgements

This work is part of the EC-project SESA (Spelt, a recovered crop for sustainable agriculture in Europe, FAIR 3-CT-96-1569) and was financed by the Swiss Federal Office for Education and Science (No. 96-0174-2). The authors thank Prof. C.-U. Hesemann and Dr H. Radic (University of Hohenheim, Stuttgart, Germany) for the protein analysis and data and Dr R. D'Ovidio (University of Tuscia, Viterbo, Italy) for the probe pUTVAy, S. Valarezo, S. Boller and E. Sager for technical assistance, and to Prof. H. F. Utz for providing the computer packages PLABSTAT and PLABQTL.

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