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Quantitative trait loci for lodging resistance in a segregating wheat × spelt population

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Abstract Lodging can strongly affect both the grain yield and the quality of wheat. Lodging represents a quantitative trait and is difficult to assess on a phenotypic basis. Marker-assisted selection (MAS) could therefore become an important tool in breeding for lodging resistance. In this study, we mapped and characterised quantitative trait loci (QTLs) for lodging resistance, as well as morphological traits correlated with lodging, in a segregating population of 226 recombinant inbred lines derived from the cross of the lodging-resistant wheat variety Forno with the susceptible spelt variety Oberkulmer. Lodging, plant height, leaf width, leaf-growth habit, culm stiffness, culm swinging, culm thickness, days to ear emergence and days to flowering were assessed in field trials at two locations in 1996 and at one location in 1997. Additionally, at one location weight and length parameters were also assessed. Plant height and culm stiffness explained 77% of the phenotypic variance of lodging in a multiple regression model over all three environments. QTL analysis of lodging and morphological parameters was based on a genetic map containing 230 loci with 23 linkage groups (2469 cM). With the method of composite interval mapping nine QTLs for lodging resistance were detected, explaining 63% of the phenotypic variance in a simultaneous fit. Seven of these QTLs coincided with QTLs for morphological traits, reflecting the correlations between these traits and lodging. In our population the most efficient way to improve lodging resistance would be by a combination of indirect selection on plant height and culm stiffness together with MAS on the two QTLs for lodging resistance which did not coincide with QTLs for morphological traits.

Key words Lodging · Morphological traits · QTL · *Triticum aestivum* · *Triticum spelta*

Introduction

Lodging in cereals is defined as a permanent displacement of the culms from their upright position. Lodging is caused by a combination of wind and rain and can be enhanced by different pathogens and pests affecting stems or roots. High-nitrogen fertilisation will favour lodging due to increased length of the lower internodes, higher fresh weight of aerial parts of the plants (Pinthus 1973), decreased culm stiffness, lower number of coronal roots and less anchorage strength (Crook and Ennos 1995). High seed-density will enhance lodging by increasing culm length and decreasing culm diameter as well as total root mass (Brady 1934; Easson et al. 1993). In wheat (*Triticum aestivum* L.), lodging can reduce grain yield by 4–20% (Briggs 1990), 30% (Pinthus 1973) or even 40% (Easson et al. 1993). In a limited range the yield losses caused by a reduction in the number of grains per ear and in the thousand-kernel weight are proportional to the percentage of lodged plants (Easson et al. 1993). Milling and

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baking quality can be considerably reduced due to the increased moisture content of the grain and pre-harvest sprouting (Baier 1965). In lodged plants the contamination with mycotoxins produced by *Fusarium* species on the ears can be significantly increased (Langseth and Stabbetorp 1996).

Lodging resistance is an important goal of cereal breeding. The introgression of dwarfing genes and the use of chemical growth regulators in intensive agriculture has decreased the risk of lodging in wheat (Pinthus 1973). However, very short plants can favour the epidemic spread of fungal diseases resulting in an undesired increase of fungicide use. In the scope of an ecological agriculture, the application of chemical growth regulators and of fungicides should be reduced. Therefore, the lodging resistance breeding goal has kept its importance. This is particularly true for spelt (*Triticum spelta* L.), where old landraces and most varieties available on the market have long and weak culms and are therefore highly susceptible to lodging. Wheat × spelt crosses are often made to improve lodging resistance in spelt breeding (Schmid and Winzeler 1990). Breeding for lodging resistance is difficult, because it is a quantitative trait, i.e. several genes are involved and environmental conditions have an important effect on the expression of the trait.

Scoring for lodging resistance in the field can be inconsistent as incidences causing lodging can occur at very different stages of plant development or not at all (Atkins 1938). Therefore, it has always been a major aim of research to establish methods to assess lodging resistance independent of weather conditions (Heyland 1960). Most of the studies conducted so far have tried to find morphological traits that are correlated with lodging and could be used as indirect selection parameters. In wheat, morphological traits of aerial parts of the plant that are correlated with lodging resistance are: plant height (Atkins 1938; Bauer 1963; Pinthus 1967), culm weight (Atkins 1938) or culm diameter (Zuber et al. 1999). Depending on the plant material employed, not all of these authors found significant correlations between these traits and lodging resistance. In a set of 15 spring wheat breeding lines, Zuber et al. (1999) were able to explain about 50% of the phenotypic variance of lodging resistance by culm weight per cm, and 48% by culm diameter. Another group of traits which can be used as predictors for lodging resistance are mechanical culm parameters. Correlations between lodging resistance and the critical bending stress of culms were found in wheat (Heyland 1960) and barley (Jezowski et al. 1987). However, other authors did not find any significant correlation between lodging and mechanical parameters of the culms in wheat (Atkins 1938; Crook and Ennos 1994), barley (Clark and Wilson 1933; Murthy and Rao 1980) or rye (Oehme 1989). Thus, no single trait, or group of traits, has proven to be generally reliable as an index of lodging resistance.

With the possibility of establishing genetic maps and of calculating the most likely positions of quantitative trait loci (QTLs) on these maps, molecular markers for lodging resistance can be identified. Consequently, marker-assisted selection (MAS) would become an important tool to improve lodging resistance in cereals. Only few studies have been published so far which localised QTLs in wheat, e.g. QTLs for resistance against pathogens (Faris et al. 1997; Nelson et al. 1997, 1998) and QTLs for grain characters (Anderson et al. 1993; Sourdille et al. 1996). There are three studies which localised QTLs for lodging resistance in barley doubled-haploid populations (Backes et al. 1995; Hayes et al. 1995; Tinker et al. 1996). Champoux et al. (1995) localised QTLs for root-morphology characters in rice, which could be correlated with lodging resistance. However, these authors only investigated correlations between these characters and drought avoidance.

To our knowledge, no QTLs for lodging resistance have been localised in wheat or spelt. In this study we have mapped and characterised QTLs for lodging resistance and for morphological traits of aerial parts of the plants correlated with lodging in a segregating wheat × spelt population. Messmer et al. (1999) established a comprehensive genetic map of this population which was used as a basis for the QTL analysis. The objectives of our study were: (1) to assess morphological traits influencing lodging resistance, (2) to estimate the number and the genomic positions of QTLs with significant effects on lodging and on correlated morphological traits, and (3) to elucidate the genetic basis of the phenotypic correlations between these traits based on coincidences between QTLs.

Materials and methods

The plant population studied consisted of 226 F_5 recombinant inbred lines (RILs) originating from a cross between the Swiss winter wheat Forno and the Swiss winter spelt Oberkulmer. The parental varieties differ strongly in their morphological characteristics as well as in lodging resistance. The progeny of the cross was propagated as bulks up to the F_5 generation in which 226 single plants were randomly selected.

Field trials

The 226 RILs of Forno × Oberkulmer were cultivated in three different environments: in 1996 at Reckenholz (Rec96) and Eschikon (Esc96) and in 1997 at Rossberg (Ros97). The RILs were grown together with 11 spelt and seven wheat standard cultivars and three replicated entries of the parental varieties (250 entries) in a rectangular lattice design with two replications and ten genotypes per incomplete block. The material was sown in 7-row (6-row in Rec96) drill plots (6 m^2) with 350 naked seeds/m^2. Fertilisation and chemical plant protection was carried out according to standard agricultural practice in Switzerland. Nitrogen fertilisation was at 100 kg N/ha. Foot-rot diseases were prevented by applying 1 l/ha of Sportak (Bayer) between DC 31 and 33 (decimal code according to Zadoks et al. 1974).

Phenotypic assessment in the field

Scoring for lodging was done six times between end of stem elongation (DC 37) and harvest in Rec96 and Esc96, and nine times between ear emergence (DC 51) and harvest in Ros97. The scoring scale ranged from 1 (all plants in the plot completely upright) to 9 (all plants in the plot completely lodged), depending on the deviation of the plants from the vertical and on the percentage of lodged plants per plot. For example, a score of 5 was set when 50% of the plants in a plot were lodged at an angle of at least 45° from the vertical. The morphological traits that were assessed in all three environments are shown in Table 1. Single scorings were averaged to reduce the scoring error.

Based on the findings of Zuber et al. (1999) the following additional traits were measured in Rec96 on 84 randomly selected RILs in both replications: culm length (CL) in cm, culm fresh weight (CW) in g, ear length (EL) in cm, ear fresh weight (EW) in g, length of flag leaf (FL) in cm, length of second leaf (LL), total leaf fresh weight (LW) and culm diameter (CD) in mm. From culm weight and culm length, culm weight per cm ($\mathrm{Cw \cdot cm^{-1}}$) was calculated. For these measurements, ten tillers from each plot were randomly selected and cut at ground level at flowering (DC 69). The measurements were done on a fresh weight basis, because fresh weight was better correlated with lodging than dry weight (Zuber et al. 1999). However, fresh weight can vary with changing weather conditions (Neenan and Spencer-Smith 1975; Easson et al. 1993). Weight and length measurements were therefore obtained in less than 20 min after cutting the tillers, whereas CD was measured in the field at ten randomly selected strong tillers in the middle of the first aboveground internode at early milk development (DC 73).

Statistical analysis of field data

Lattice analysis of single environments and analysis of variance over environments were both performed with the program PLABSTAT (Version 2M, Utz 1995). Adjusted entry means were used to compute the analysis of variance across environments. The variance components were computed by considering the effects of environment and genotype as random. Estimates of the variance components σ_g^2 (genetic variance), σ_e^2 (environment variance), σ_{ge}^2 (genotype × environment interaction variance) and σ^2 (error variance) were obtained. Heritabilities (h^2) were calculated on an entry mean basis according to Hallauer and Miranda Fo (1981). The segregation of the 226 RILs was tested for normality for the assessed traits. Phenotypic correlation coefficients were calculated among all assessed traits on an entry mean basis across the three environments. Multiple regression models for lodging with all morphological traits as variables were calculated for single environments and across environments with the stepwise procedure of SAS (SAS Institute 1988).

For the length and weight parameters additionally assessed on 84 RILs in Rec96 an analysis of variance was carried out over the two replications. Estimates of variance components σ_g^2 (genetic variance), σ_r^2 (replication variance), σ^2 (error variance) were also obtained. Heritabilities were estimated on a plot level. Simple correlations with lodging and multiple-regression models for lodging were calculated on the basis of entry means.

QTL analysis

The marker genotype of the 226 RILs was assessed with 176 RFLP probes and nine wheat microsatellites. For the construction of the genetic map, linkage analysis was performed with the program MAPMAKER (Lander et al. 1987) using the Haldane mapping function (Haldane 1919) as described by Messmer et al. (1999). After the removal of closely linked marked loci (<1 cM) the genetic map used for QTL mapping comprised 182 marker loci (2469 cM) with an average marker density of 13.6 cM. This covers about 2/3 rds of the wheat genome (Messmer et al. 1999). Genotypes with more than 10% of the markers being heterozygous, or deviating bands indicating outcrossing, were excluded from the QTL data set. The QTL analysis was performed with 204 genotypes by the software-package PLABQTL (Utz and Melchinger 1996) based on composite interval mapping (CIM). Co-factors were assessed by the procedure cov SELECT. The threshold for the detection of a QTL was fixed at a LOD value of 3.0. The explained phenotypic variance of each QTL and of multiple regression models with all detected QTLs were calculated. Based on the QTL analysis for lodging, averaged over Rec96 and Esc96, predicted values for every genotype were determined. A simple regression was obtained between these predicted values and the observed values in Ros97. QTLs were tested for digenic epistatic effects. To analyse if QTLs found for lodging resistance were closely linked to, or had pleiotropic effects on, the other assessed traits, comparative QTL mapping for all traits was done. Since the assignment of linkage groups to physical chromosomes was not in every case completely clear, it is advisable for the localisation of QTLs to refer to flanking markers rather than to physical chromosomes (Messmer et al., 1999).

Results

Phenotypic trait analysis

The population means for lodging were 4.9 (Rec96), 4.8 (Esc96) and 2.5 (Ros97). The lodging scores of the two locations in 1996 were more correlated to each other ($r = 0.80$) than to the location in 1997 ($r = 0.65$–0.70). This indicates that the year effect was stronger than the effect of the location. In 1997 we had lower canopy densities than in 1996, due to the very dry conditions in

Table 1 Morphological traits assessed in three environments on a plot basis for 226 RILs from the cross Forno × Oberkulmer

Trait	Short form	Scale	Growth stage (DC)[a]	Number of assessments
Plant height	PHT	cm	69	1
Leaf width	LWH	1 (thin leaf)–3 (broad leaf)	39–49	1–2
Leaf growth habit	LGH	1 (upright leaf)–3 (hanging leaf)	39–49	1
Culm stiffness	CST	1 (stiff culm)–5 (weak culm)	39–59	1–6
Culm swinging	CSW	1 (short swing. time)–5 (long swing. time)	49–69	1–4
Culm thickness	CTH	1 (thin culm)–4 (thick culm)	59–69	1–2
Ear emergence	EEM	Days	57	1
Flowering	FLO	Days	61	1

[a] Decimal code according to Zadoks et al. 1974

early spring resulting in less tillering. In addition, the weather conditions were less favourable for lodging in 1997. Therefore, the differentiation was good for lodging-resistant RILs in 1996, and for lodging-susceptible RILs in 1997. The distribution of lodging score averaged over all three environments did not deviate significantly from a normal distribution and showed transgression. The traits culm thickness (CTH), days to ear emergence (EEM) and days to flowering (FLO) were also normally distributed, whereas the distributions of plant height (PHT), leaf width (LWH), leaf-growth habit (LGH), culm stiffness (CST) and culm swing (CSW) deviated significantly from a normal distribution. For the morphological traits the correlations between the three environments were in the same range as for lodging (data not shown). All traits showed transgressive segregation (Table 2), even those with big differences between the parental lines. Estimates for σ_g^2 and for σ_{ge}^2 among the RILs were highly significant ($P < 0.01$) for all traits (Table 2). However, genotype × environment interactions were small compared to the genotypic effects. Heritability estimates were very high (> 0.90) for lodging, PHT, LGH, CSW, EEM and for FLO, and somewhat smaller for LWH, CST and for CTH. Therefore, we consider our phenotypic data averaged over environments as a reliable basis for QTL mapping.

The traits PHT, CST and CSW showed the highest phenotypic correlation coefficients with lodging compared to all other traits (Table 3). Apart from LWH all traits showed highly significant ($P < 0.01$) correlations among each other. To analyse these interrelations we calculated multiple-regression models (Table 4). In all three environments PHT and CST were the two main factors explaining between 55% and 73% of the phenotypic variance of lodging. Other traits such as LGH, CSW and EEM had significant, but small, effects on lodging. Averaged over all three environments PHT, CST and LWH explained 78% of the phenotypic variance of lodging.

Except for culm length (CL) the weight and length parameters additionally assessed on 84 RILs in Rec96 showed clearly lower heritabilities than the traits assessed on all 226 RILs (Tables 5 and 1). The correlations between most of these traits and lodging were highly significant. In a multiple-regression model for lodging with all 17 traits as variables for 84 RILs, most of the phenotypic variance of lodging was explained by culm stiffness ($R^2_{part} = 48\%$), plant height ($R^2_{part} = 13\%$) and leaf-growth habit ($R^2_{part} = 8\%$). The only weight

Table 2 Means of parents Forno (Fo) and Oberkulmer (Ok) and 226 RILs derived from their cross, plus standard deviations (SD), estimates of variance components and heritabilities over three environments for lodging, plant height (PHT), leaf width (LWH), leaf-growth habit (LGH), culm stiffness (CST), culm swinging (CSW), culm thickness (CTH), days to ear emergence (EEM) and days to flowering (FLO) averaged across three environments

Trait	Score	Fo	Ok	Parent. mean	Mean 226 RILs	SD	Min.	Max.	σ_g^2	σ_{ge}^2	h^2
Lodging	[1–9]	1.5	5.1	3.3	4.1	1.0	1.5	6.9	1.1[a]	0.2[a]	0.91
PHT	[cm]	102	148	125	134	11	107	160	151[a]	11[a]	0.96
LWH	[1–3]	1.9	1.8	1.8	2.0	0.4	1.0	3.1	0.2[a]	0.0[a]	0.89
LGH	[1–3]	1.3	2.6	1.9	2.0	0.6	0.9	3.0	0.3[a]	0.1[a]	0.91
CST	[1–5]	1.3	3.8	2.5	3.1	0.9	1.0	5.0	0.8[a]	0.2[a]	0.87
CSW	[1–5]	1.8	4.7	3.3	3.5	1.1	1.0	5.2	1.1[a]	0.1[a]	0.93
CTH	[1–4]	2.3	2.5	2.4	2.5	0.6	0.9	4.0	0.3[a]	0.0[a]	0.88
EEM	[Days]	155	161	158	159	2	154	165	3.4[a]	0.3[a]	0.96
FLO	[Days]	159	162	160	161	1	157	166	0.9[a]	1.4[a]	0.95

[a] Variance component was significant at the 0.01 probability level

Table 3 Phenotypic correlation coefficients averaged across three environments among plant height (PHT), leaf width (LWH), leaf-growth habit (LGH), culm stiffness (CST), culm swinging (CSW), culm thickness (CTH), days to ear emergence (EEM), days to flowering (FLO) and lodging for 226 RILs from the cross Forno × Oberkulmer

Trait	PHT	LWH	LGH	CST	CSW	CTH	EEM	FLO
LWH	0.00							
LGH	0.37**	– 0.05						
CST	0.62**	– 0.32**	0.61**					
CSW	0.79**	– 0.14*	0.41**	0.75**				
CTH	– 0.22**	0.49**	– 0.28**	– 0.57**	– 0.57**			
EEM	– 0.43**	0.12	– 0.24**	– 0.21**	– 0.45**	0.45**		
FLO	– 0.43**	0.08	– 0.28**	– 0.22**	– 0.43**	0.44*	0.95**	
Lodging	0.79**	– 0.07	0.51**	0.79**	0.76**	– 0.34**	– 0.27**	– 0.29**

*, ** Correlation was significant at the 0.05 and 0.01 probability level, respectively

and length parameter with a significant effect ($P < 0.05$) in this model was ear fresh-weight ($R^2_{\text{part}} = 2\%$). The final multiple regression model with these four traits as variables explained 72% of the phenotypic variance of lodging. Without ear fresh-weight the model still explained 70% of the phenotypic variance of lodging. The additional information of ear fresh-weight was too small to justify any further assessment of this trait. All the other weight and length parameters did not explain any additional part of the phenotypic variance of lodging. These traits were therefore ignored for further assessment and analysis.

Table 4 Multiple regression models for lodging for single environments (Rec96, Esc96 and Ros97) and for the average over three environments (average) with the partial explained phenotypic variance (part. R^2) of lodging and the sum of the explained phenotypic variance (Σ R^2) for 226 RILs from the cross Forno × Oberkulmer

Trait	part. R^2	Σ R^2	Sign.
Rec96			
Plant height	0.44	0.44	**
Culm stiffness	0.15	0.59	**
Leaf-growth habit	0.06	0.65	**
Culm swinging	0.01	0.67	**
Ros97			
Plant height	0.69	0.69	**
Culm stiffness	0.04	0.73	**
Days to ear emergence	0.02	0.76	**
Leaf-growth habit	0.00	0.76	*
Culm thickness	0.01	0.77	*
Esc96			
Plant height	0.45	0.45	**
Culm stiffness	0.11	0.55	**
Leaf-growth habit	0.04	0.59	**
Days to ear emergence	0.02	0.61	**
Leaf width	0.01	0.62	*
Average			
Plant height	0.63	0.63	**
Culm stiffness	0.15	0.77	**
Leaf width	0.01	0.78	**

*,** Value was significant at the 0.05 and 0.01 probability level, respectively

QTLs for lodging

Thirteen QTLs (Rec96), eight QTLs (Esc96) and eight QTLs (Ros97) for lodging were detected with a LOD > 3.0 in composite interval mapping (Fig. 1). Individual QTLs explained between 6.6 and 32.1% of the phenotypic variance in composite interval mapping involving the co-factors and had a partial R^2 between 2.1 and 27.8% in the simultaneous fit. Models fitting all QTLs explained 59.2% (Rec96), 44.0% (Esc96) and 62.2% (Ros97) of the phenotypic variance. Five QTLs were consistent over three environments, an additional three were consistent over two environments (Fig. 1). The additive effects of the simultaneous fit varied considerably between environments. The additive effects of the QTLs on 3A (54–64 cM) and on 5A (90–102 cM) varied between 0.23 (Ros97) and 0.43 (Rec96), and between 0.19 (Ros97) and 0.42 (Rec96), respectively. Averaged over all three environments nine QTLs were detected explaining 62.7% of the phenotypic variance (Table 6). Three of these QTLs had major effects (part. $R^2 > 20\%$). Lodging resistance can therefore be considered as a polygenic trait with major effects of a few single genes. At six QTLs the allele for better lodging-resistance was from the short, stiff, lodging-resistant parent Forno (Fo), at the three others from Oberkulmer (Ok) (Table 6). The predicted values based on the QTLs analysis for lodging, averaged over Rec96 and Esc96, explained 44.4% of the observed phenotypic variance in Ros97.

One significant epistatic effect was detected between the QTLs on chromosome 2AS and on 7BL explaining 6.2% of the phenotypic variance for lodging in a multiple-regression model with all QTLs as variables. At both of these QTLs the allele for better lodging resistance was from Oberkulmer. The distributions for

Table 5 Means of parents Forno (Fo) and Oberkulmer (Ok) and 84 RILs derived from their cross, plus standard deviations (SD), estimates of variance components, heritabilities on plot level and correlation to lodging for culm length (CL), culm fresh weight (CW), ear length (EL), ear fresh weight (EW), length of flag leaf (FL), length of second leaf (LL), total leaf fresh weight (LW), culm diameter (CD) and culm weight per cm ($Cw \cdot cm^{-1}$), averaged over two replications in Rec96

Trait	Unit	Fo	Ok	Parent. mean	Mean 84 RILs	SD	Min.	Max.	σ^2_g	σ^2_r	h^2	Corr. to lodging
CL	[cm]	94.5	143.8	119.2	125.6	9.6	98.0	146.5	123.4**	– 0.1	0.88	0.62**
CW	[g]	5.25	8.32	6.79	7.25	0.98	4.65	9.60	0.82**	0.15**	0.74	0.40**
EL	[cm]	9.5	15.0	12.3	12.1	2.1	8.0	21.5	3.1**	0.1*	0.69	0.36**
EW	[g]	1.80	2.02	1.91	1.91	0.31	1.30	2.75	0.05**	0.00	0.56	0.49**
FL	[cm]	23.5	26.0	24.8	25.5	2.6	19.0	34.0	3.7**	0.1	0.54	0.34**
LL	[cm]	30.0	33.8	31.9	32.1	3.6	25.0	53.0	4.9**	0.1	0.41	0.29**
LW	[g]	1.17	1.50	1.34	1.45	0.32	0.90	2.45	0.04**	0.00	0.38	– 0.01
CD	[mm]	2.94	3.15	3.05	3.09	0.24	2.59	3.66	0.03**	0.01**	0.53	– 0.16
$Cw \cdot cm^{-1}$	[mg/cm]	55.6	57.9	56.8	57.7	6.4	38.0	74.0	20.2**	8.53**	0.51	0.07

*,** Value was significant at the 0.05 and 0.01 probability level, respectively

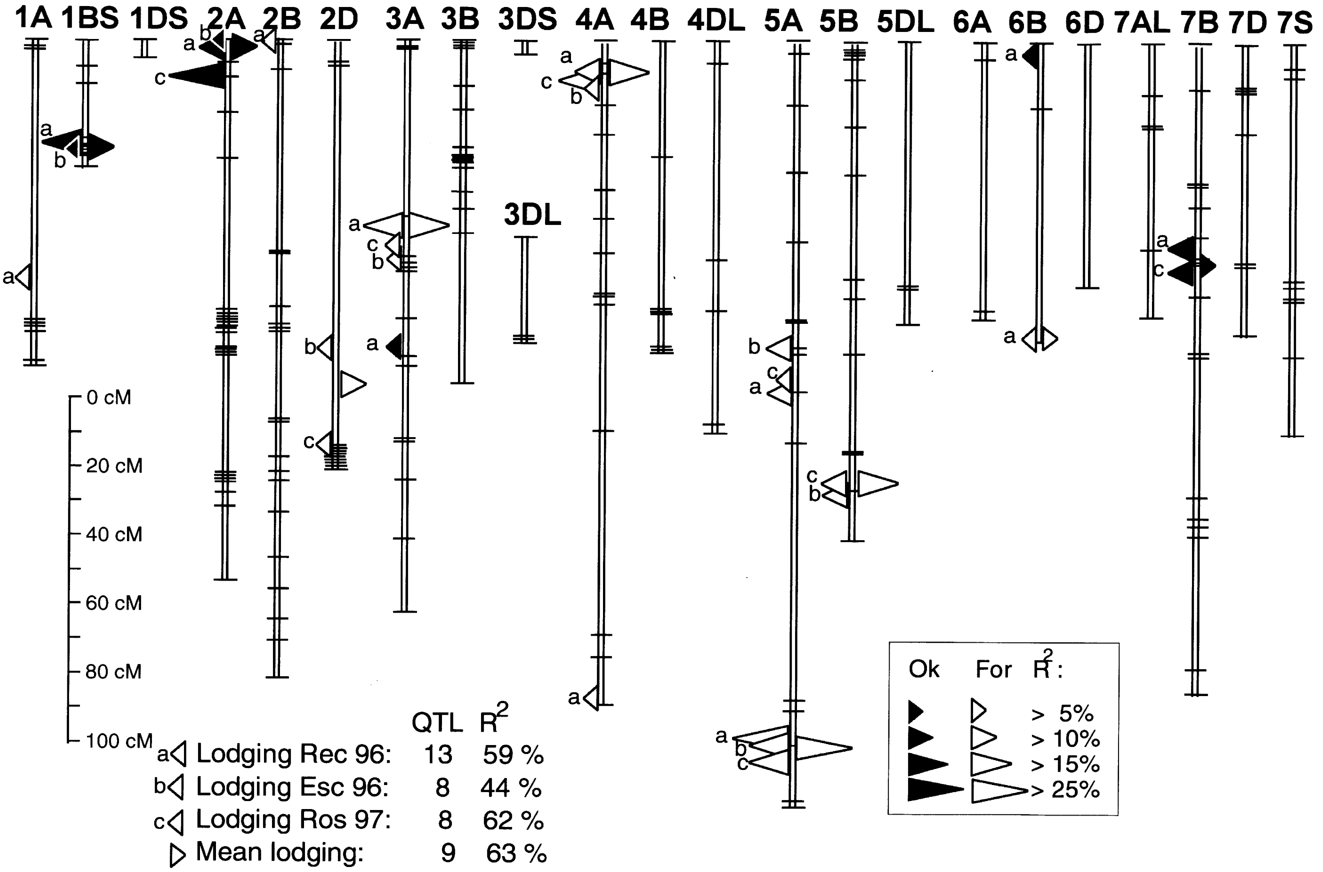

Fig. 1 Positions of significant (LOD > 3.0) QTLs for lodging on the genetic map of 204 RILs derived from the cross Forno × Oberkulmer. QTLs for lodging in single environments are indicated by *triangles to the left* side of the chromosomes (a = Rec96, b = Esc96, c = Ros97). QTLs for lodging over all environments are indicated by *triangles to the right* side of the chromosomes. The *size* of the triangles indicates the explained phenotypic variance (R^2) of a single QTL. *White or black triangles* indicate that the allele for improved lodging resistance was inherited from Forno or from Oberkulmer, respectively

lodging of RILs with different allele combinations at these two QTLs are shown in Fig. 2. The means of the four distributions were 3.65 (43 genotypes with the Ok allele at the flanking marker loci *Xpsr958* and *Xpsr566c* on 2AS and at the flanking markers *Xpsr927* and *Xpsr350* on 7BL), 3.77 (28 genotypes with the Ok allele on 2AS and the Fo allele on 7BL), 3.90 (51 genotypes with the Fo allele on 2AS and the Ok allele on 7BL) and 4.83 (26 genotypes with the Fo allele on 2AS and on 7BL), respectively.

QTLs for plant height

Averaged over all three environments 11 QTLs (LOD > 3.0) for plant height were detected (Table 7). Individual QTLs explained between 7.9 and 31.4% of the phenotypic variance in composite interval mapping involving the co-factors, and had a partial R^2 between 1.5 and 29.6% in the simultaneous fit. At six loci the allele for shorter plants came from the short parent Forno, at five loci from Oberkulmer. A model fitting all QTLs explained 72.6% of the phenotypic variance. No significant epistatic effects between QTLs were detected. Five QTLs for plant height were coincident with the QTLs for lodging (Table 6). At these QTLs the allele for shorter plants corresponded to the allele for better lodging resistance.

QTLs for culm stiffness

Averaged over three environments eight QTLs (LOD > 3.0) for culm stiffness were detected (Table 7). At five loci the allele for stiffer culms was from the stiffer parent Forno, at three loci from Oberkulmer. Individual QTLs explained between 7.5 and 28.0% of the phenotypic variance in composite interval mapping involving the co-factors and had a partial R^2 between 6.6 and 25.5% in the simultaneous fit. A model fitting all QTLs explained 58.1% of the phenotypic variance. No significant epistatic effects between QTLs were detected. Six QTLs for culm stiffness were located at the same place as the QTLs for lodging (Table 6). At these

QTLs the allele for stiffer culms corresponded to the allele for better lodging resistance.

QTLs for other traits

For the other traits we found between 8 and 12 QTLs (Table 7). For all traits both parents contributed positive and negative alleles. For LGH and for EEM there were several coincidences with QTLs for lodging (Table 6). At these loci the allele for upright leaves and for later ear emergence, respectively, corresponded to the allele for better lodging resistance. For the other traits there was less coincidence with QTLs for lodging and the alleles were in some cases opposite to the phenotypic correlation.

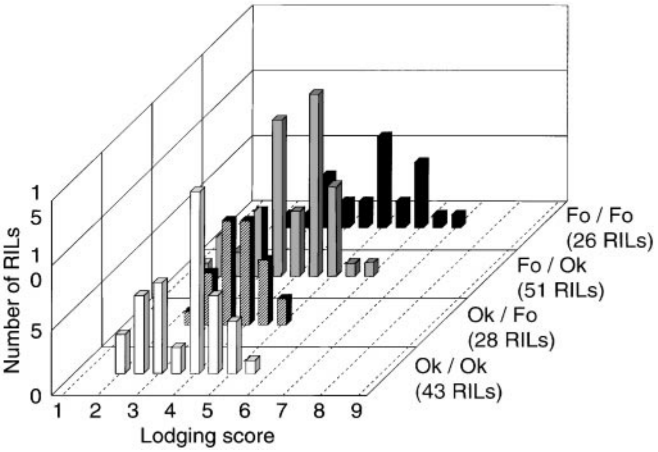

Fig. 2 Distribution of lodging scores averaged over three environments (Rec96, Esch96 and Ros97). A total of 148 RILs derived from the cross Forno × Oberkulmer were classified by alleles (*Fo* = Forno allele; *Ok* = Oberkulmer allele) at flanking marker loci of the QTLs for lodging on the chromosomes 2AS (*Xpsr958*, *Xpsr566c*) and 7BL (*Xglk549*, *Xpsr927*). At both QTLs Oberkulmer contributed the allele for better lodging resistance. The first named allele is the one on 2AS, the second on 7BL. The number of RILs for each class is indicated in *brackets*

Discussion

Genetic basis of lodging resistance

The parents of the analysed population differed significantly in lodging resistance. Therefore, the RILs showed extreme variability for this trait. Wheat × spelt crosses are used to introgress lodging resistance from bread wheat into spelt germplasm, because there is very little variation for this trait within the gene pool of spelt (Schmid and Winzeler 1990). For spelt breeding, genes of wheat which increase lodging resistance but with little reduction in the typical long culm of spelt are of special interest.

We found nine QTLs for lodging distributed across the whole genome. No RILs were more lodging-resistant than the resistant parent Forno, because there was no scorable differentiation below the lodging score of Forno (1.5). In comparison to our investigation a similar number of QTLs for lodging resistance has been found in two studies with barley doubled-haploid lines. Hayes et al. (1995) identified six QTLs in 150 lines explaining 72% of the variation. Tinker et al. (1996) found six QTLs in 146 lines with composite interval mapping. In both studies each parent contributed positive and negative alleles for lodging, and the population showed transgressive segregation. In contrast to our study, Backes et al. (1995) obtained only three QTLs for lodging in 250 barley doubled-haploid lines explaining 26% of the genotypic variance. Transgressive segregation was evident, although the better allele at each QTL was contributed by the better parent.

The only significant epistatic effect for lodging was between the QTL on chromosome 2AS and the one on

Table 6 QTLs for lodging and coincidences with QTLs for plant height (PHT), culm stiffness (CST), leaf width (LWH), leaf-growth habit (LGH), days to ear emergence (EEM) and culm thickness (CTH), averaged over three environments for 204 RILs from the cross Forno × Oberkulmer with the position on chromosomes, support interval (cM), flanking marker loci, additive effects and explained phenotypic variance (R^2) for single QTLs

QTLs for lodging					Coincident QTLs					
Chromosome	cM (support interval)	Flanking marker loci	R^2	Additive effect[a]	PHT	CST	LWH	LGH	EEM	CTH
1BS	28–**32**–34	*Xpsr949–Xgwm18*	12%	– 0.25	Shorter	Stiffer	Broader			
2AS	0–**2**–6	*Xpsr958–Xpsr566c*	15%	– 0.33	Shorter	Stiffer	Broader	More erect	Later	Thicker
2D	74–**100**–122	*Xpsr933b–Xglk529a*	15%	0.48						
3AS	42–**54**–58	*Xpsr598–Xpsr570*	21%	0.36		Stiffer				Thinner
4AS	8–**10**–14	*Xgwm397–Xglk315*	23%	0.38	Shorter	Stiffer		More erect		
5AL	202–**208**–212	*Xpsr918b–Xpsr1201a*	31%	0.49	Shorter	Stiffer	Narrower	More erect	Later	Thicker
5BL	124–**128**–136	*Xpsr370–Xpsr580b*	20%	0.45		Stiffer	Broader	More erect		
6BL	56–**86**–86	*Xpsr964–Xpsr142*	7%	0.10						
7BL	56–**64**–70	*Xpsr927–Xpsr350*	7%	– 0.29	Shorter				Later	

[a] Positive value: allele from Forno for better lodging resistance; negative value: allele from Oberkulmer for better lodging resistance

Table 7 QTLs for morphological traits: plant height (PHT), culm stiffness (CST), culm swing (CSW), leaf width (LWH), leaf-growth habit (LGH), culm thickness (CTH), days to ear emergence (EEM) and days to flowering (FLO), averaged over three environments for 204 RILs from the cross Forno × Oberkulmer with the position on chromosomes, support interval (cM), additive effects (Add.), explained phenotypic variance (R^2) for single QTLs and total explained phenotypic variance in a simultaneous fit

Chromosome	PHT		CST		CSW		LWH		LGH		CTH		EEM		FLO	
	R^2	Add.[a]	R^2	Add.	R^2	Add.	R^2	Add.	R^2	Add.	R^2	Add.	R^2	Add.	R^2	Add.
1A	7.9%	1.43					6.6%	0.13	12.1%	0.13			7.5%	−0.40	12.3%	−0.42
cM[b]	82–**86**–92						82–**88**–94		82–**86**–92				82–**84**–92		82–**84**–90	
1B	13.3%	−0.84	12.0%	−0.24			14.0%	0.11								
cM	30–**32**–36		30–**34**–36				28–**32**–34									
2A	29.3%	−3.50	28.0%	−0.36	33.2%	−0.45	9.3%	0.13	6.6%	−0.12	31.2%	0.29	9.8%	0.59	8.7%	−0.37
cM	8–**10**–14		2–**4**–8		6–**8**–10		6–**8**–16		0–**0**–6		2–**8**–10		0–**2**–8		130–**142**–152	
2A													9.5%	−0.31		
cM													78–**80**–84			
2B											13.2%	0.23	8.7%	0.54	8.0%	−0.27
cM											82–**88**–98		82–**88**–100		0–**2**–8	
2B															12.3%	0.35
cM															126–**130**–134	
2D					7.2%	0.20										
cM					62–**96**–122											
3A			8.4%	0.40							14.7%	0.16			7.1%	−0.29
cM			28–**44**–58								62–**64**–68				90–**94**–108	
3B							19.7%	−0.13	11.1%	−0.10	11.3%	−0.09				
cM							50–**54**–56		40–**44**–48		50–**54**–78					
4A	22.5%	4.53	18.2%	0.33	21.1%	0.40			16.4%	0.18						
cM	8–**12**–16		8–**12**–16		8–**12**–16				8–**10**–16							
4A	12.6%	−1.99			11.7%	−0.22					16.0%	−0.21	13.8%	−0.46	15.4%	−0.36
cM	50–**54**–58				76–**78**–88						190–**194**–194		178–**182**–188		176–**182**–188	
4B	8.8%	3.09									12.9%	0.26	9.8%	−0.11		

4D			7.5%	−0.18												
cM			112–**114**–114													
5A			9.8%	0.23	9.4%	0.17			11.2%	0.15					11.1%	−0.43
cM			72–**84**–90		42–**52**–72				32–**42**–52						64–**76**–88	
5A	31.4%	4.63			14.7%	0.18			9.0%	0.22						
cM	100–**104**–108				102–**104**–108				68–**80**–86							
5A	23.1%	4.09	27.0%	0.45	53.1%	0.66	14.9%	0.08	6.6%	−0.21	37.6%	−0.33	22.0%	−0.54	15.8%	−0.35
cM	202–**206**–212		202–**208**–214		204–**206**–210		174–**192**–196		94–**100**–110		202–**208**–212		204–**206**–112		202–**206**–212	
5B	13.9%	−2.87					7.3%	−0.08			11.1%	−0.16	9.2%	−0.39	6.6%	−0.24
cM	2–**4**–8						0–**2**–4				32–**40**–50		18–**24**–32		12–**20**–34	
5B			8.2%	0.26	19.7%	0.36	11.2%	−0.13	6.7%	0.12			6.7%	0.23		
cM			124–**130**–138		124–**128**–136		108–**120**–126		122–**128**–138				70–**76**–80			
5D									6.6%	0.11						
cM									70–**72**–78							
6A	11.7%	2.02					7.2%	−0.14								
cM	4–**6**–24						78–**80**–80									
7A											11.1%	0.21			14.4%	0.51
cM											20–**24**–32				18–**30**–40	
7A											8.2%	−0.13				
cM											68–**76**–78					
7B	18.3%	−2.38							6.6%	0.16	8.8%	−0.12	8.5%	0.54	20.5%	0.49
cM	58–**64**–68								32–**42**–50		184–**188**–188		50–**56**–60		26–**34**–44	
7D									16.4%	−0.15						
cM									52–**64**–66							
R^2 (simultaneous fit)	**72.6%**		**58.1%**		**74.6%**		**59.5%**		**52.8%**		**63.1%**		**50.2%**		**60.7%**	

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[a] additive effects were estimated from the simultaneous fit of all QTLs. Positive effects indicate that the Oberkulmer allele contributes to a higher value, i.e. taller plants, weaker culms, broader and less-erect leaves, later ear emergence and flowering, thicker culms

[b] The first and the third numbers indicate the support interval, the number printed in bold indicates the position of the highest LOD score of the QTL. QTLs with overlapping support intervals and/or with less than 20 cM between the peaks can not definitively be separated from each other and are therefore set in the same line

7BL which explained a relevant part of the phenotypic variation (part. $R^2 = 6.2\%$). The phenotypic distributions of the RILs subdivided by the alleles at the two QTLs suggest a duplicate gene action between these QTLs, i.e. if at least one of the loci carried the positive allele, lodging resistance was improved. The presence of the positive alleles at both loci did not improve lodging resistance any further. A similar type of epistatic effect had been found in maize between QTLs for resistance against European corn borer (Schön et al. 1993) and between QTLs for grey leaf spot resistance (Maroof et al. 1996). To reliably detect interactions between QTLs, very large populations are needed (Tanksley 1993). Gallais and Rives (1993) suggested that the QTLs detected with the strongest effects are likely to be those with little epistasis. This may be the reason why in our study we found no significant epistatic effects between QTLs except for lodging.

Most of the QTLs for lodging were consistent over environments, but the additive effects of the simultaneous fit varied considerably between environments. This can be explained by the effect of the year. Averaged over all three environments lodging was correlated with days to ear emergence ($r = -0.27$) as well as with days to flowering ($r = -0.29$), i.e. in our population late genotypes were more lodging-resistant. However, in single environments lodging was not always correlated with days to flowering. In Rec96, the correlation of days to flowering to lodging was highly significant ($r = -0.37$) whereas in Ros97 we found no significant correlation. The point of time of the weather event which causes lodging plays an important role in the reaction of the genotype. Baier (1965), Clark and Wilson (1933) and Heyland (1960) found that the degree of lodging is dependent on the plant growth stage at which a critical weather event occurs. Sensitive growth stages were milk development (Bauer 1963), grain filling (Crook and Ennos 1994) or ripening (Neenan and Spencer-Smith 1975). Despite this dependence on weather events, our results suggest that the QTLs for lodging resistance estimated over different environments are reliable predictors for other environments.

Morphological traits as indirect selection parameters for lodging resistance

In our population, a large amount of the variance for lodging could be predicted by the morphological traits plant height and culm stiffness ($R^2 = 77\%$). The RILs showed an extreme variance for plant height. It is therefore not surprising that plant height showed the highest correlation of all traits to lodging ($r = 0.79$). The generally better lodging resistance of short varieties has been reported for barley (Murthy and Rao 1980: $r = 0.56$; Stanca et al. 1979: $r = 0.63$), rye (Oehme 1989: $r = 0.77$ at DC 67/69) and wheat (Bauer 1963: $r = 0.90$; Pinthus 1967: $r = 0.62$). Plant height is probably the best trait for an indirect assessment of lodging resistance. However, in plant material that has been selected for plant height, and therefore has a smaller variation, the correlations can be lower or even insignificant (Zuber et al. 1999). These authors found a correlation of 0.49 between lodging and plant height in 15 spring wheat lines, which was insignificant. Inconsistent correlations between plant height or stem length and lodging in spring wheat varieties were also reported by Atkins (1938).

In the analysed population, the mechanical parameter culm stiffness was as highly correlated to lodging as plant height. Culm stiffness is easy to assess by hand scoring. Some cereal breeders use this trait as an indirect selection parameter for lodging resistance. The reproducibility of its scoring is very good, as evident from the high correlation ($r = 0.86$) of the average of three independent scorings by two persons in Ros97. Scorings of culm stiffness can be done two to three times before ear emergence. By averaging the scorings the reliability of data can be increased.

For mechanical culm parameters, such as bending or breaking strength, results from the literature are conflicting. Jezowski et al. (1987) found significant ranking correlations between lodging in barley and the bending stress of culms, and Young's modulus (a measure of culm elasticity), respectively. However, other authors did not find any significant correlation between lodging and mechanical parameters of the culms in wheat (Atkins 1938; Crook and Ennos 1994), barley (Clark and Wilson 1933; Murthy and Rao 1980) or rye (Oehme 1989). These studies are based on measurements on single culms, while our hand scoring of culm stiffness was done on a drill plot basis and therefore included several further characteristics such as biomass, culm length and canopy density.

Genetic basis of phenotypic correlations of lodging to morphological traits

Of the total of nine QTLs for lodging, seven coincided with QTLs for morphological traits, reflecting the correlations between these traits and lodging. However, the two QTLs on chromosomes 2D and 6BL had no coincident QTLs with any other trait. An improvement of the population for these two genes could therefore not be achieved by an indirect selection via morphological traits. MAS for these two QTLs would be a more-efficient approach than a phenotypic assessment of lodging itself. Additionally, there were two QTLs for lodging on chromosomes 3AS and 5BL at the same place as the QTLs for culm stiffness. There was no coincidence between these QTLs and QTLs for plant height. With MAS for these loci lodging resistance could be increased without decreasing plant height. Thus, these loci are very interesting for spelt breeding.

Coincidence of QTLs for plant height with major dwarfing genes

In cereals plant height is known to be determined by many genes. In wheat almost all 21 chromosomes were found to contribute to genetic variation for plant height in the case of the substitution of lines of Cappelle-Desprez into Chinese Spring (Snape et al. 1977). About 20 major genes for height reduction, so called dwarfing genes (*Rht* genes), are known (McIntosh et al. 1995). Five of the known dwarfing genes are located on chromosomes where we found QTLs for plant height: On chromosome 2A there is *Rht7* (Worland et al. 1980), on 4BS *Rht1* and *Rht3* (these are two alleles of the same locus) (McVittie et al. 1978; Gale and Youssefian 1985), on 5AL *Rht12* (Sutka and Kovacs 1987) and on 7BS *Rht9* (Law et al. 1981). Of these *Rht* genes *Rht1* and *Rht3* are gibberellic acid-insensitive (GA) genes, i.e. dwarf mutants of this type show a reduced response or complete insensitivity to applied GA. Besides these known GA-insensitive genes there are probably others on 5B and 7B (Börner et al. 1992), where we also found QTLs for plant height. It is possible to determine the presence of GA-insensitive genes by differences in the reaction to a treatment with GA. Based on experiments done by Dr. A. Börner (Institute of Plant Genetics and Crop Research Gatersleben, Germany) we can exclude the presence of GA-insensitive genes in the population we analysed (Börner, personal communication). However, it is possible that some of the QTLs for plant height in the analysed population are alleles of GA-sensitive dwarfing genes that can not be detected by the seedling test (Börner et al. 1996). Korzun et al. (1997) mapped *Rht12* on chromosome 5AL with a genetic distance of 15 cM to *Xpsr1201*. The QTL for plant height we found on 5AL was located 14 cM apart from *Xpsr1201*. This is strong evidence for the presence of *Rht12* or else of an allelic relationship between this gene and the QTL in our population.

Perspectives for marker-assisted selection

Selection for lodging-resistant genotypes can be done via indirect selection based on the morphological traits of plant height and culm stiffness before flowering. In the analysed population the most efficient way to improve lodging resistance would be a combination of indirect selection on plant height and culm stiffness combined with MAS on the two QTLs, which do not coincide with the QTLs for morphological traits. Even though lodging resistance is a polygenic trait, single genes can still have major effects. It should be possible to introgress such genes from wheat into spelt by one or two backcrosses without strongly affecting plant height.

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