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Multiple-line cross QTL mapping for biomass yield and plant height in triticale (× *Triticosecale* Wittmack)

Katharina V. Alheit · Lucas Busemeyer · Wenxin Liu · Hans Peter Maurer ·
Manje Gowda · Volker Hahn · Sigrid Weissmann · Arno Ruckelshausen ·
Jochen C. Reif · Tobias Würschum

Abstract

Key message **QTL mapping in multiple families identifies trait-specific and pleiotropic QTL for biomass yield and plant height in triticale.**

Abstract Triticale shows a broad genetic variation for biomass yield which is of interest for a range of purposes, including bioenergy. Plant height is a major contributor to biomass yield and in this study, we investigated the genetic architecture underlying biomass yield and plant height by multiple-line cross QTL mapping. We employed 647 doubled haploid lines from four mapping populations that have been evaluated in four environments and genotyped with 1710 DArT markers. Twelve QTL were identified for plant height and nine for biomass yield which cross-validated explained 59.6 and 38.2 % of the genotypic variance, respectively. A major QTL for both traits was identified on chromosome 5R which likely corresponds to the dominant dwarfing gene *Ddw1*. In addition, we detected epistatic QTL for plant height and biomass yield which, however, contributed only little to the genetic architecture of the traits. In conclusion, our results demonstrate the potential of genomic approaches for a knowledge-based improvement of biomass yield in triticale.

K. V. Alheit, L. Busemeyer and W. Liu contributed equally to this work.

K. V. Alheit · H. P. Maurer · M. Gowda · V. Hahn ·
T. Würschum (✉)
State Plant Breeding Institute, University of Hohenheim,
70593 Stuttgart, Germany
e-mail: tobias.wuerschum@uni-hohenheim.de

L. Busemeyer · A. Ruckelshausen
Competence Centre of Applied Agricultural Engineering,
University of Applied Sciences Osnabrück, Sedanstrasse 26,
49076 Osnabrück, Germany

W. Liu
Crop Genetics and Breeding Department, China Agricultural
University, Beijing 100193, China

S. Weissmann
Saatzucht Dr. Hege GbR Domäne Hohebuch, 74638 Waldenburg,
Germany

J. C. Reif
Leibnitz Institute of Plant Genetics and Crop Plant Research
(IPK), 06466 Gatersleben, Germany

Introduction

The small grain cereal triticale (× *Triticosecale* Wittmack; $2n = 6x = 42$), a man-made wheat-rye hybrid, is considered a promising crop due to its high genetic variation for several traits of agronomic importance. It is widely adapted to abiotic stress conditions such as aluminum toxicity, drought, salinity, and acidic or waterlogged soils (Kuleung et al. 2004; Oettler 2005). With regard to biomass yield, triticale is able to produce more biomass for a comparable grain yield than other crops (Pronyk and Mazza 2011). Consequently, biomass production for industrial purposes, such as bioenergy and biofuel, can be increased without aggravating the competition with food production on arable land. Winter triticale is, therefore, ideally suited to diversify crop rotation in regions where maize is the predominant crop grown for biomass production (Gowda et al. 2011).

The development of improved varieties depends on the ability to readily phenotype numerous genotypes in the field. Biomass yield is traditionally evaluated by harvesting yield plots with a field chopper. This destructive analysis,

however, has the disadvantage that no further traits can be obtained from these plants and biomass yield is therefore not routinely assessed in plant breeding. Busemeyer et al. (2013a, b) recently reported the development of a multi-sensor platform that enables non-destructive field-based phenotyping of small grain cereals. This precision phenotyping platform has been calibrated to assess biomass yield of triticale which yielded a high prediction accuracy and heritability for the predicted biomass (Busemeyer et al. 2013a).

Results from Gowda et al. (2011) suggested plant height to be a key contributor to biomass yield in triticale while grain yield, heading time, spikes per square meter and 1,000-kernel weight contribute to a lesser extent. This study also revealed a broad genetic variation for biomass yield in triticale germplasm. To date, little is known, however, on the genetics underlying biomass yield in triticale and other small grain cereals. Busemeyer et al. (2013a) reported two major QTL for biomass yield on chromosomes 5A and 5R which were identified by association mapping in multiple families. By contrast, the genetics underlying plant height in cereals are much better understood. Plant height is a complex trait determined by many genes with small effects, but major dwarfing genes resulting in substantial reductions in height are also known and have been intensively used in breeding programs (Banaszak 2011; Börner et al. 1996, 1999a; Flintham et al. 1997; Gale and Youssefian 1985; Ren et al. 2010). The dwarfing genes identified in wheat, rye and barley appear to represent a homoeologous series in these three species (Börner et al. 1996; Ivandic et al. 1999). To the best of our knowledge, no studies on plant height and dwarfing genes are available for hexaploid triticale.

QTL mapping approaches can be employed to dissect the genetic architecture underlying complex traits and to identify QTL for marker-assisted selection programs. The extension of linkage mapping methodology towards multiple segregating families offers several advantages like, for example, an increased QTL-detection power and a higher precision of QTL position estimates (Würschum 2012). Consequently, this multiple-line cross QTL (MC-QTL) mapping approach has recently been applied to a range of diverse crops including maize, sugar beet and rapeseed (Blanc et al. 2006; Liu et al. 2012, 2013; Rebai and Goffinet 1993, 2000; Schwegler et al. 2013; Steinhoff et al. 2011, 2012a, b; Würschum et al. 2012a).

In this study, we used a large mapping population consisting of 647 doubled haploid triticale lines derived from four families evaluated in four environments and genotyped with 1710 DArT markers, to dissect the genetic architecture of biomass yield and plant height by MC-QTL mapping. In particular, the objectives of this study were to (1) identify main-effect QTL for the two traits, (2) assess the precision of QTL position estimates and the predictive power of the

identified QTL by cross-validation, and (3) investigate the contribution of epistatic interactions to the genetic architecture of plant height and biomass yield in triticale.

Materials and methods

Plant materials and field experiments

This study was based on 647 doubled haploid (DH) triticale lines (Würschum et al. 2012b) derived from four families: DH06 (131 individuals), DH07 (120), EAW74 (200), and EAW78 (196) which have been described by Alheit et al. (2011). The field experiments and the collection of biomass data have been described by Busemeyer et al. (2013a). In brief, the progenies were evaluated in partially replicated trials (Williams et al. 2011) including common checks with 960 plots per location at two locations, Hohenheim and Bohlingen (both situated in southwest Germany), in the years 2011 and 2012. Six-row plots (5 m^2) were machine sown and data recorded for plant height and biomass at the developmental stage BBCH 81 (very early dough development) (Lancashire et al. 1991). Plant height was recorded conventionally, and biomass data was obtained with the precision phenotyping platform and prediction according to a developed calibration model (Busemeyer et al. 2013a, b).

Genotypic and phenotypic analyses

The 647 mapping individuals were genotyped with DArT markers and the map positions of a high-density consensus linkage map incorporating 1,710 markers were used for analyses (Alheit et al. 2011). Phenotypic data were analyzed by ordinary lattice analysis of variance (Cochran and Cox 1957) employing a two-step approach as suggested by Möhring and Piepho (2009). In the first step, the phenotypic data of each environment were analyzed separately based on the statistical model

$$y_{ijk} = \mu + g_i + r_j + b_{jk} + e_{ijk}$$

where y_{ijk} is the phenotypic performance of the ith entry in the jth replication in the kth incomplete block, μ an intercept term, g_i the genetic effect of the ith genotype, r_j the effect of the jth replication, b_{jk} the effect of the kth incomplete block in the jth replication, and e_{ijk} the residual. Except b_{jk} all effects were treated as fixed. The adjusted entry means of each genotype and one divided by the squared standard error as weighting factor were used in the second step for the analysis across environments with the following model

$$y_{ij} = \mu + g_i + \text{env}_j + g_i{:}\,\text{env}_j + e_{ij}$$

where y_{ij} is the adjusted entry mean of the ith genotype at the jth environment estimated in the first step, g_i the genetic effect of the ith genotype, env_j the effect of the jth environment, g_i: env_j the genotype by environment interaction, and e_{ij} the residual. For the analysis of single families, we used dummy variables which indicate the membership of a genotype to the respective family. Variance components were determined by the restricted maximum likelihood (REML) method assuming a random model. Best linear unbiased estimates (BLUEs) were estimated across environments assuming fixed effects for the genotype. Heritability (h^2) on an entry-mean basis was estimated from the variance components as the ratio of genotypic to phenotypic variance (Knapp et al. 1985). All statistical analyses were performed using ASReml 3.0 (Gilmour et al. 2009).

Multiple-line cross QTL mapping

For multiple-line cross QTL (MC-QTL) mapping (Blanc et al. 2006), we applied a model assuming specific QTL effects for every family (disconnected model) as this has recently been shown to perform well (Schwegler et al. 2013, Steinhoff et al. 2011). In brief, the model was

$$Y = JM + X'_q B'_q + \sum_{c \neq q} X'_c B'_c + \varepsilon$$

where Y denotes a $N \times 1$ column vector of BLUE values of phenotypic data of N progenies coming from F families, J is a $N \times F$ matrix whose elements were 0 or 1 according to whether or not individual i belonged to family f and M is a $F \times 1$ vector of family specific means. $X'_q (X'_c)$ denotes an $N \times F$ matrix containing the expected number (ranging from 0 to 2) of allele k for each individual in family f at QTL q (cofactor c), and $B'_q (B'_c)$ is a $F \times 1$ vector of the expected allele substitution effects of QTL q (cofactor c) in family f. ε denotes the vector of the residuals.

Cofactor selection was performed using PROC GLMSELECT implemented in the statistical software SAS (SAS Institute 2008). Testing for presence of a putative QTL in an interval was performed using a likelihood ratio test with the statistical software R (R Development Core Team 2005). LOD thresholds of 4.7 and 4.6 for plant height and biomass yield, respectively, were used corresponding to an experiment-wise type I error of $P < 0.10$, based on 2,000 permutations (Doerge and Churchill 1996). QTL were declared as overlapping between both traits if they fell within an arbitrarily defined 10-cM interval surrounding the QTL.

A full two-dimensional scan for pair-wise interactions was performed based on the comparison of a full versus a reduced model (Steinhoff et al. 2012b). In the full model, all cofactors selected plus the main effects of the two loci analyzed were included, whereas in the reduced model the interaction term between the two loci analyzed was excluded. Following the suggestion of Holland et al. (2002), the chosen α level of 0.05 was divided by the number of possible independent pair-wise interactions between chromosome regions, assuming two regions per chromosome ($P < 5.8 \times 10^{-5}$). The circular plots illustrating the epistatic interactions were created with Circos (Krzywinski et al. 2009).

The proportion of the genotypic variance explained by all detected QTL was estimated across the four families as R^2_{adj}/h^2, where h^2 refers to the heritability of the trait (Utz et al. 2000). The support interval of a QTL was defined as a LOD fall-off of 1.0 expressed as position on the chromosome in centimorgans (cM) (Lander and Botstein 1989) and cofactors were excluded within a distance to the marker interval under consideration smaller than 10 cM.

Cross-validation

To evaluate the results of QTL detection, a fivefold cross-validation approach with genotypic sampling was performed following Liu et al. (2013). In brief, the data set was randomly subdivided into five subsets, while maintaining the relative contribution of the individual families in each subset. Four of the five genotypic samples were used as estimation set (ES) for QTL detection, localization and estimation of their genetic effects. The remaining lines in the test set (TS) served as an independent sample used for validation of the QTL results from the ES and to obtain unbiased estimates of the genotypic variance explained by the QTL ($p_{G\text{-}TS}$). The random sampling of genotypes into ES and TS was repeated 600 times. The proportion of the genotypic variance of the detected QTL in the ES ($p_{G\text{-}ES}$) was compared to that explained in the TS ($p_{G\text{-}TS}$) to calculate the bias as $p_{G\text{-}ES} - p_{G\text{-}TS}$, and the relative bias as $1 - (p_{G\text{-}TS}/p_{G\text{-}ES})$.

Results

For both biomass yield and plant height, we observed significant ($P < 0.01$) genotypic variances and genotype × environment interaction variances (Table 1). The heritability amounted 0.95 for plant height and 0.85 for biomass yield. The phenotypic correlation between plant height and biomass yield was 0.86 in the entire population and ranged between 0.59 and 0.91 within the four families (all $P < 0.001$). The means of the parents of the crosses differed to varying degrees for plant height (Δ 2.1–13.6 cm) as well as for biomass yield (Δ 1.3–19.4 dt ha^{-1}) (Fig. 1). Orthogonal contrasts of the means of the parental lines and the means of the populations were not significantly different for both traits. The trait distributions approximately

Table 1 Summary statistics and QTL mapping results for plant height (cm) and grain yield (dt ha^{-1}) from fivefold cross-validation

Parameter	Plant height	Biomass yield
Min	77.5	81.3
Mean	110.5	149.7
Max	135.5	187.1
σ_G^2	131.1**	232.8**
$\sigma_{G \times E}^2$	13.7**	43.9**
σ_e^2	18.7	173.4
h^2	0.95	0.85
QTL$_{DS}$	12	9
p_{G-DS}	74.8	62.8
p_{G-ES}	77.8	57.0
p_{G-TS}	59.6	38.2
Bias	18.2	18.8
Relative bias	23.4	33.0

Genotypic variance (σ_G^2), genotype by environment interaction variance ($\sigma_{G \times E}^2$), error variance (σ_e^2), and heritability (h^2)

** Significant at the 0.01 probability level. Number of QTL detected in the full data set (QTL$_{DS}$), proportion of explained variance in percent in the data set (p_{G-DS}), the estimation set (p_{G-ES}), and in the test set (p_{G-TS}), and the bias in the estimation of the proportion of explained genotypic variance

followed a normal distribution except for family EAW78 which especially for plant height showed a bimodal distribution (Fig. 1). For both traits, DH lines showed transgressive segregation compared to the phenotypes of the parental lines. Taken together, the phenotypic data present an excellent basis to dissect the genetics underlying plant height and biomass yield in triticale.

The multiple-line cross QTL mapping across the four DH families comprising a total of 647 individuals revealed twelve QTL for plant height and nine QTL for biomass yield (Table 1; Fig. 2). The proportion of genotypic variance explained by these QTL amounted 74.8 % for plant height and 62.8 % for biomass yield. The proportion of genotypic variance explained by individual QTL ranged from 1.0 to 42.0 % for plant height and from 2.2 to 35.6 % for biomass yield (Table 2) and the major QTL for both plant height and biomass yield was located on chromosome 5R. The QTL effects showed considerable variation across families. We employed a fivefold cross-validation approach to obtain unbiased estimates of the predictive power of the QTL for both traits (Table 1). The cross-validated proportion of explained genotypic variance was 59.6 % for plant height and 38.2 % for biomass yield. The relative bias was higher for biomass yield with 33.0 % as compared to 23.4 % for plant height.

The QTL frequency distributions revealed that some of the QTL, including the major QTL on chromosome 5R, were identified in more than 40 % of the runs (Fig. 3). By contrast, few QTL detected with the full data set were only detected in less than 10 % of the runs (e.g., biomass yield QTL on chromosome 4R). In general, the QTL frequency distributions showed narrow peaks at the QTL positions.
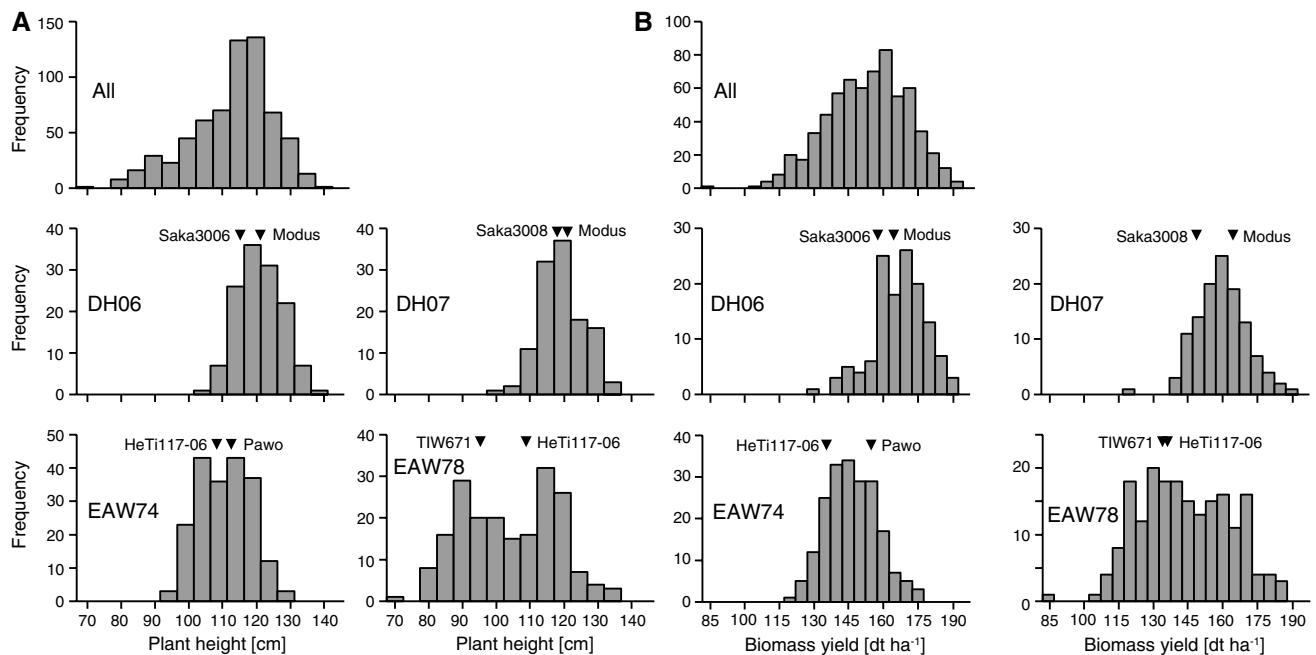

Fig. 1 Frequency distributions of phenotypic data for (**a**) plant height and (**b**) biomass yield across all genotypes and for the single families. *Arrowheads* indicate the phenotypic value of the respective parents
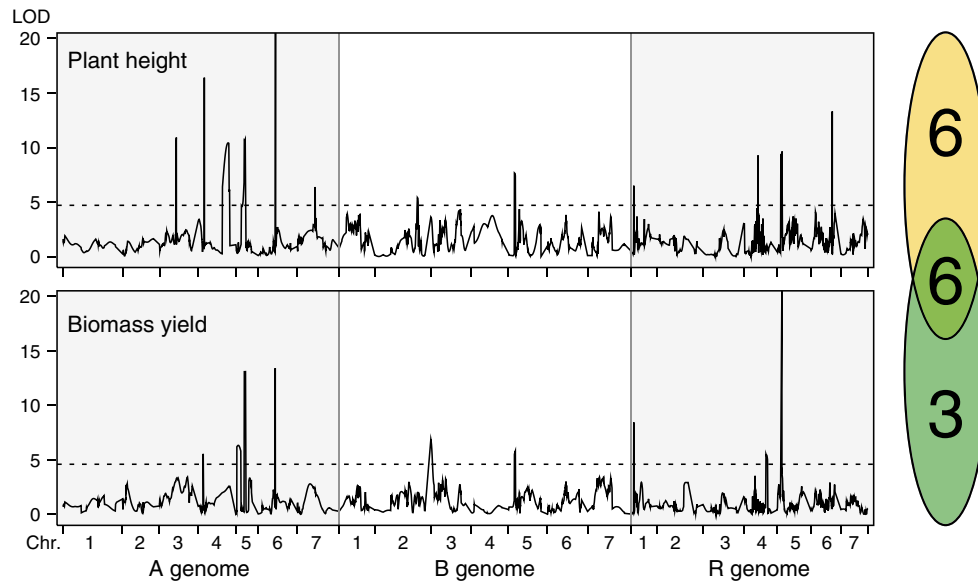
Fig. 2 LOD curves from MC-QTL mapping for plant height and biomass yield. The *dashed horizontal line* indicates the significance threshold. *Venn diagram* indicates overlapping and trait-specific QTL

Table 2 QTL detected for plant height and biomass yield

| Nearest marker (distance to QTL cM)	LOD	Chr	Position cM (SI)	p_G	QTL effect			
					DH06	DH07	EAW74	EAW78
Plant height (cm)								
wPt-8041 (0.0)	10.9	3A	57.6 (55.9–57.7)	2.1	−1.0	2.2	−1.9	1.3
wPt-3349 (0.0)	16.4	4A	20.9 (20.7–21.0)	3.2	2.8	2.6	0.0	0.0
wPt-7391 (2.1)	10.4	4A	101.7 (92–104.4)	2.1	−2.2	−1.1	−0.7	−1.6
wPt-8096 (1.0)	10.8	5A	31.8 (28.3–32.3)	2.2	−1.4	−1.9	−1.2	−1.9
wPt-0902 (0.0)	38.6	6A	58.2 (57.9–58.5)	8.7	0.0	0.0	5.0	1.7
wPt-1961 (0.0)	6.4	7A	61.5 (61.1–61.7)	1.4	0.0	2.0	0.9	1.1
wPt-2106 (3.2)	5.4	2B	144.5 (144.0–147.8)	1.0	0.0	−1.4	−0.6	−1.3
wPt-1420 (0.0)	7.7	5B	21.2 (20.8–24.8)	2.3	−1.2	0.0	2.1	−2.0
rPt-402007 (0.0)	6.5	1R	10.6 (10.2–10.6)	0.9	0.0	0.0	0.0	2.0
rPt-399305 (0.0)	9.3	4R	48.5 (48.2–48.6)	1.8	3.5	−1.4	0.0	2.2
rPt-509721 (0.0)	9.6	5R	17.0 (17.0–18.0)	42.0	−0.9	0.0	−1.4	−11.4
rPt-508661 (0.0)	13.3	6R	72.7 (72.7–72.8)	2.7	−1.2	−1.5	1.3	3.3
Biomass yield (dt ha^{-1})								
tPt-512917 (0.0)	5.6	4A	17.1 (16.8–17.8)	2.2	1.4	3.3	0.0	2.2
wPt-1052 (4.6)	6.3	5A	8.6 (3.3–17.3)	2.6	4.3	−2.6	−2.5	0.0
wPt-8096 (0.0)	13.1	5A	32.8 (28.3–33.6)	5.5	−5.4	−2.5	0.0	−4.8
tPt-513137 (0.0)	13.4	6A	57.7 (57.5–57.9)	5.5	−1.5	0.0	4.7	2.8
wPt-9496 (0.0)	6.9	3B	0.0 (0.0–3.8)	2.5	−2.3	4.5	1.6	2.5
wPt-6348 (1.0)	5.8	5B	24.3 (20.8–24.8)	2.6	0.0	2.1	2.8	−2.6
rPt-402007 (0.0)	8.4	1R	10.6 (10.2–10.6)	3.3	0.0	0.0	2.8	3.8
rPt-508464 (0.0)	5.5	4R	75.4 (74.9–81.2)	2.2	2.4	0.0	0.0	2.9
rPt-400153 (1.3)	70.8	5R	14.4 (13.8–16.3)	35.6	0.0	0.0	−2.2	−14.4
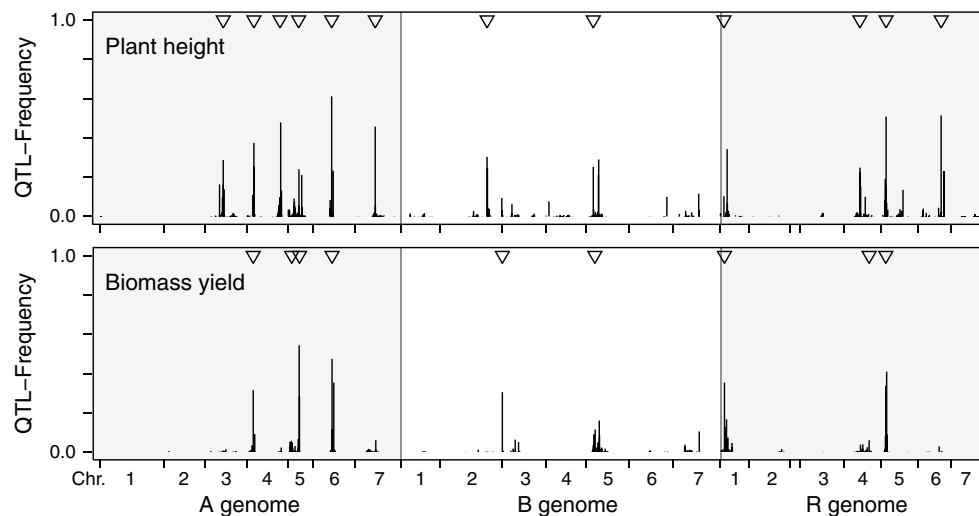
Fig. 3 Frequency distributions of QTL detected in fivefold cross-validation for plant height and biomass yield. *Arrowheads* indicate the positions of QTL detected in the full data set
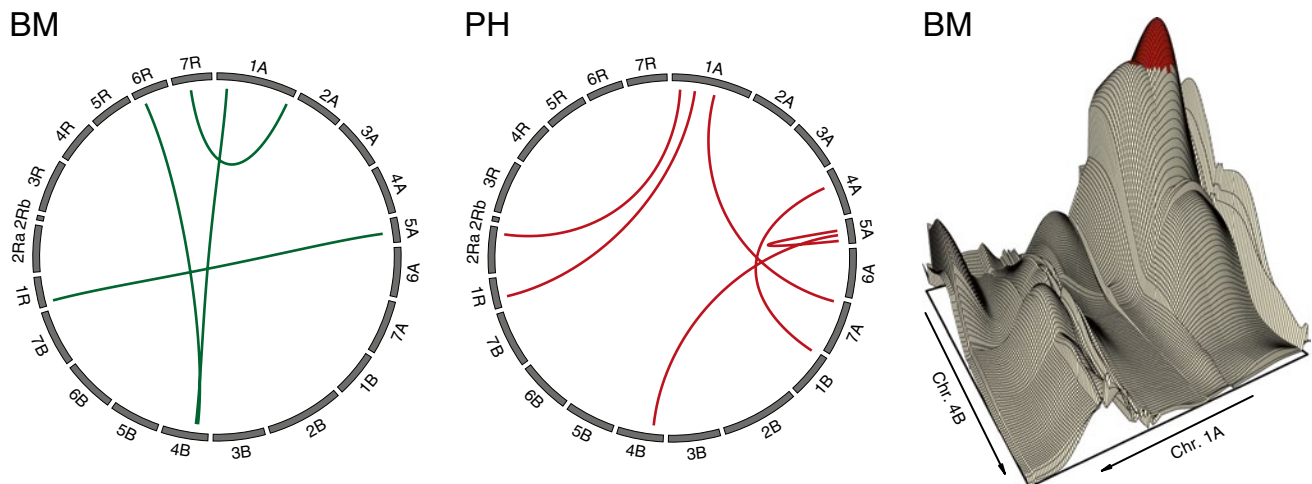

Fig. 4 Epistatic interactions for biomass yield and plant height. The epistatic QTL for biomass yield involving chromosomes 1A and 4B is shown exemplarily as epistatic interaction landscape where *red* indicates significant $-\log_{10}$ (P values)

The full two-dimensional genome scan revealed six and four epistatic QTL for plant height and biomass yield, respectively (Fig. 4). For the epistatic QTL affecting biomass yield, involving regions on chromosomes 1A and 4B, the epistatic interaction landscape is exemplarily visualized in Fig. 4. The proportion of genotypic variance explained by these epistatic QTL ranged from 0.6 to 1.1 % for plant height and from 1.3 to 1.7 % for biomass yield.

Discussion

The combined analysis of multiple biparental families offers a number of advantages as compared to QTL mapping in single populations and has consequently become increasingly popular in recent years (Blanc et al. 2006; Myles et al. 2009; Rebai and Goffinet 1993; Verhoeven et al. 2006; Würschum 2012). In this study, we used data of four partially connected DH families to unravel the genetic architecture of biomass yield and plant height in triticale.

Phenotypic properties of the mapping population

One of the main prerequisites for QTL detection with a high power is the precise estimation of phenotypic values (Liu et al. 2013). Plant height was measured conventionally with a heritability of 0.95 which is in agreement

with results from triticale (Herrmann 2007; Oettler et al. 2005), rye (Miedaner et al. 2010, 2012a) and wheat (Khan et al. 2003; Teich 1984). By contrast, biomass yield was obtained based on multi-sensor measurements by a precision phenotyping platform and subsequent prediction with a sensor-fusion calibration model (Busemeyer et al. 2013a). This yielded a high heritability of 0.85 which is in accordance with previous studies on biomass yield in rye (Miedaner et al. 2010, b) and maize (Grieder et al. 2012a, b). Thus, precision phenotyping as applied here is an attractive approach to non-invasively determine biomass yield in small grain cereals with high accuracy and heritability. The major advantage of this non-invasive approach, especially in breeding programs, is that it enables the assessment of additional traits on the same plots.

For plant height, only the parents of family EAW78 differed considerably in their phenotypic values, while for biomass yield substantial differences were found between the parents of DH07 and EAW74 (Fig. 1). However, these differences between the parents were not reflected in the genotypic variances which confirms results of Miedaner et al. (2012a) for complex traits in rye. This can be explained by the observed transgressive segregation for both traits in all families suggesting that the parents carry in part complementary QTL which are newly combined in their progeny. For family EAW78, a bimodal distribution was observed for plant height indicating that a major plant height gene is segregating in this family. In triticale, well-known dwarfing genes, originating from wheat or rye (Börner et al. 1996, 1999b), can result in substantial height differences as observed for the two parents of this cross. The observed high positive correlation between both traits suggests that plant height must be considered as major contributor to biomass yield in triticale which warrants a joint analysis of both traits and a comparison of their underlying QTL.

Detection of main-effect QTL for plant height

Plant height in small grain cereals is a complex trait controlled by many genes (Börner et al. 1996, 1999b; Flintham et al. 1997; Gale and Youssefian 1985; Miedaner et al. 2011, 2012a; Ren et al. 2010). We identified 12 main-effect QTL for plant height which cross-validated explained considerable 59.6 % of the genotypic variance (Table 1). This high proportion of explained genotypic variance can mainly be attributed to two QTL, the QTL on chromosome 6A and the major QTL on chromosome 5R (Table 2). It must be noted, that the latter showed the strongest QTL effect in family EAW78 suggesting that the allele with the strong effect on plant height only segregates in this family. The joint analysis across multiple families as employed here permits the detection of QTL with large effects segregating

in a single family, but also of QTL with small effects segregating in several of the families which are only detectable by the combined power across families. The observed bimodal distribution of plant height (Fig. 1) supports the assumption of a major QTL segregating in family EAW78. Furthermore, the parent of this cross, TIW671 or cultivar 'Pigmej', is known as very short triticale type, probably as a result of it carrying a dwarfing gene. In rye, this chromosome has been reported to harbor a major plant height QTL at the relative position on the chromosome comparable to the QTL identified here and we, therefore, speculate that the QTL detected on chromosome 5R might represent the dominant dwarfing gene *Ddw1* (Börner et al. 1999b; Korzun et al. 1996). Another QTL located on chromosome 5A might represent the dwarfing gene *Rht12*, a potential homeolog of *Ddw1* (Börner et al. 1996), demonstrating the possible combination of major plant height QTL from wheat and rye in triticale. Taken together, our results illustrate the quantitative inheritance of plant height in triticale but also demonstrate the contribution of single major QTL. The confirmation of the identified major QTL as *Ddw1* and its fine-mapping warrant further research.

Detection of main-effect QTL for biomass yield

Even though the exploitation of crop biomass holds great potential, little is known until now about the genetics of biomass yield in small grain cereals. We have recently reported the detection of biomass yield QTL in the population underlying this study (Busemeyer et al. 2013a). The biometrical model applied in the previous study is based on identity-by-state and has been show to be rather conservative with regard to QTL detection (Würschum et al. 2012c). Here, we used MC-QTL mapping which is an identity-by-descent approach and the higher proportion of explained genotypic variance realized with the detected QTL illustrates that MC-QTL mapping is well suited for QTL analysis in the underlying data set with four partially connected families. A total of nine QTL were identified for biomass yield explaining 62.8 % of the genotypic variance, thus substantially exceeding the results from the previous approach where the identified QTL explained only 28.5 % of the genotypic variance (Busemeyer et al. 2013a). This corroborates previous findings of Liu et al. (2012) who showed that identity-by-state (association mapping) and identity-by-descent (MC-QTL mapping) approaches each possess specific properties. As expected for complex traits, the cross-validated proportion of genotypic variance was lower as compared to that in the full data set but still amounted to considerable 38.2 %. As for plant height, a major QTL was identified in the same region on chromosome 5R (Table 2). In addition, two further QTL explaining more than 5 % were detected on chromosomes 5A and

6A. Busemeyer et al. (2013a) also reported QTL for biomass yield in triticale, but only on chromosomes 5A and 5R. In summary, this analysis identified several QTL and revealed that biomass yield is mainly controlled by small effect QTL.

Contribution of epistasis

Epistasis refers to interactions between the alleles at two or more genetic loci (Carlborg and Haley 2004) and has recently been shown to contribute to the genetic architecture of complex traits in crops (Buckler et al. 2009; Liu et al. 2012; Reif et al. 2011; Steinhoff et al. 2012b; Würschum et al. 2013). It must be noted that the QTL-detection power for epistatic QTL depends even more on the population size than for main-effect QTL. The comparably large mapping population underlying this study enabled the detection of six epistatic QTL for plant height and four for biomass yield. The proportion of genotypic variance explained by these epistatic QTL averaged 0.9 % for plant height and 1.5 % for biomass yield which is smaller than the average of the respective main-effect QTL (5.9 and 6.9 %, respectively). Thus, epistasis contributes to the genetic architecture of both traits albeit to a minor extent.

Consequences for plant breeding

A recent study has identified grain yield, heading time, spikes per square meter, 1,000-kernel weight, and early plant height as key variables to predict early biomass yield (Gowda et al. 2011). The high correlation between biomass yield and plant height observed in our study, confirms plant height as a major contributor to biomass yield. We consequently observed a high congruency between QTL detected for the two traits with six of the nine biomass yield QTL also being identified as plant height QTL, including the major QTL on chromosome 5R (Fig. 2). Possible reasons for this colocalization of QTL for plant height and biomass yield include: (1) two closely linked genes each affecting a separate trait; (2) one gene with a pleiotropic effect; or (3) one gene with a single function that initiates a sequence of causally related events (Lebreton et al. 1995; Liu et al. 2013).

For marker-assisted selection, the QTL positions must be estimated with high precision to minimize the probability of recombinations between the QTL and the marker used for selection. The QTL frequency distributions revealed narrow peaks for the majority of the identified QTL illustrating the reliability of the QTL position estimates (Fig. 3). Another important criterion to assess the prospects of marker-assisted selection is the proportion of genotypic variance explained by the detected QTL. Cross-validation is an approach to obtain unbiased estimates of this parameter (Liu et al. 2013; Schön et al. 2004). The cross-validated

proportion of explained genotypic variance was substantially higher for plant height (59.6 %) than for biomass yield (38.2 %) which is likely due to the higher complexity of the latter. While single QTL explaining a sufficiently high proportion of the genotypic variance may be used in marker-assisted selection, the combined predictive power of all identified QTL was still limited. This is concordant with the quantitative nature of the traits which are controlled by many small effect QTL that escape detection in QTL mapping. Future research should aim at evaluating the performance of genomic selection to improve these traits as this approach also considers QTL with small effects. In summary, our data show that marker-assisted selection based on the QTL detected by MC-QTL mapping, or potentially genomic selection, hold potential for a knowledge-based improvement of biomass yield in triticale.

Conclusions

In this study, we report the first MC-QTL mapping in triticale which identified several QTL for plant height and biomass yield. The high correlation between the two traits confirms plant height as a major contributor to biomass yield and several of the biomass yield QTL have also been identified as plant height QTL. A major plant height QTL was detected on chromosome 5R and is likely to represent the dominant dwarfing gene *Ddw1* which is well known from rye breeding. Furthermore, our results showed that epistatic interactions contribute to a minor extent to the genetic architecture of plant height and biomass yield in triticale. In summary, genomic approaches, like MC-QTL mapping applied here, hold the potential for a knowledge-based breeding of triticale cultivars with improved biomass yield.

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