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Quantitative-trait loci (QTL) mapping of
important agronomical traits of the grain and
biomass production in winter rye
(*Secale cereale* L.)

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Abbreviations

ANOVA	analysis of variance
BBCH	decimal code of phenological growth stages, which is divided into principal and secondary growth stages based on the cereal code developed by Zadoks et al. (1974); the abbreviation BBCH derives from Biologische Bundesanstalt, Bundessortenamt and Chemical industry (Meier 2001)
cM	centimorgan
CMS	cytoplasmic male sterile
CV	cross validation
DA	discrimination ability
DArT	Diversity Arrays Technology
DMY	dry matter yield
EG	early growth
GBS	genotyping by sequencing
G x E	genotype by environment interaction
G x I	genotype by irrigation interaction
G x I x E	genotype by irrigation by environment interaction
GS	genomic selection
GY	grain yield
H201	parent 1 of Pop-D
H202	parent 2 of Pop-D
HT	heading time
LOD	limit of detection
LSD	least significant difference
MAS	marker assisted selection
MET	multi-environment trial
NIL	near isogenic lines
PA	prediction ability
PH	plant height
PH 1	plant height measured in EC 32
PH 2	plant height measured in EC51-55
PH 3	plant height measured before harvest
Pop-A	population developed by KWS CEREALS GmbH, intrapool
Pop-B	population developed by KWS CEREALS GmbH, intrapool
Pop-C	population developed by KWS CEREALS GmbH, interpool
Pop-D	population developed by HYBRO Saatzucht GmbH, interpool
QTL	quantitative trait loci
R ²	phenotypic variance explained by detected QTL
RFLP	restriction fragment length polymorphism
SNP	single nucleotide polymorphisms
SPM	spikes per square meter
SSR	simple sequence repeats
TGW	thousand-grain weight

1. General introduction

Rye (*Secale cereale* L.) is an important crop in Central and Eastern Europe and mainly grown in temperate regions, such as Germany, Russia, Belarus, Ukraine, and Poland with approximately 5.4 million hectares worldwide in 2012 (“FAO,” 2014). The highest production quantity was obtained in 2012 in Germany and Poland with 3.9 and 2.87 million tones, respectively. The largest area designated to rye was 1.4 million hectares in 2012 in the Russian Federation. (“FAO,” 2014). Rye is primarily cultivated as a winter cereal in regions with sandy and marginal soils. In comparison to other crops rye has a relatively highly tolerance to biotic and abiotic stress factors, which mainly occur on light soils (“ECOPORT Database, *Secale cereale*,” 2002; Hoffmann, 2008). Two heterotic groups (Petkus and Carsten pool) and an effective system of cytoplasmatic male sterility (CMS) with high pollen fertilization offers effective hybrid breeding (Geiger and Miedaner, 1999). Today more than 70% are hybrid varieties in Germany, which are used for food and feed and, more recently, became important for biogas production (Geiger and Miedaner, 2009). These variations in utilization demand different requirements for breeding goals. Besides increasing grain yield (GY) for food-related products, traits such as baking quality, sprouting resistance, thousand-grain weight (TGW), and composition of grain ingredients are important. For feed a high protein content is preferred, while pentosan content should be low (Boros, 2007). For biogas production high dry matter yield (DMY) with a high methane yield per hectare is important (Amon et al., 2007; Hübner et al., 2011).

1.1. Rye as a renewable energy source

The importance of renewable bioenergy resources will increase in the future. Due to climate change and finite fossil resources, the use of plants, plant products and plant waste for energy production will play an important role. Thus, the EU is projected to generate one-third of their energy from sustainable and regional biomass sources (European Commission, 2008).

Maize (*Zea mays* L.) is the most important energy crop in Germany with making up to 79% of the total biomass and 0.8 million hectares in 2013 (Weiland, 2006;

“Deutsches Maiskomitee e.V. (DMK),” 2014). With the use of other crops, such as sugar beet, triticale and rye, for bioenergy production new opportunities have arisen. Moreover, it is favorable to use a wide range of different energy crops for regions where crop rotation is utilized, maize monocultures are not economic and two harvests annually could increase the total biomass yield per hectare (Hübner et al., 2011). Even though rye will never reach the yield potential of maize if both crops are grown under normal or good soil and climate conditions (Oslaj et al., 2010; Hübner et al., 2011), in regions where it is not economic to grow maize for bioenergy production rye is an alternative. In this case rye would also not conflict with the production of food related agriculture crops. Furthermore, the use of winter hybrid rye varieties provides the opportunity to increase total biomass yield per year and decrease the erosion of soils and nutrient loss compared to maize cultivation in the summer only.

Successful production of biogas is dependent on the methane yield per hectare (Amon et al., 2007). Harvest at late milk ripening results in the highest DMY and methane yield combined with low lignin content. Consequently, breeding goals for high DMY are important for the effective use of rye for biogas production (Hübner et al., 2011). Rye has a wide range of genetic variation for biomass yield (Miedaner et al., 2010, 2012b), but little is known in modern breeding programs about an effective way to improve biomass yield for the use of biogas.

1.2. Drought tolerance and yield stability

Climate change has a worldwide effect on the agricultural production systems and an influence on cultivated crops (Ceccarelli et al., 2007). Despite climate change being controversial and different studies not being able to accurately predict the local climate condition in future, the effects of extreme weather events on cereal crop production have increased during the last decade and Europe has been effected more often by regional heatwaves and rainfall deficit, which has caused yield reduction (Ciais et al., 2005). The average winter conditions are predicted to get wetter while summer terms are predicted to get dryer and hotter (DWD, 2014). Particularly dry spring seasons have a strong negative influence on crop development and yield. This effect is even stronger on light and sandy soils

as predominant in Lower Saxony and East Germany, where rye is predominantly cultivated (Hoffmann, 2008). Dry spring and summer seasons do not regularly occur but in the last two decades they have become more prevalent. In 1996, 2007, 2009, 2010 and 2011 and 2014 April was among the driest months within the last two decades, compared to the long term average (DWD, 2014). In general an ideal drought tolerant genotype should give high yields under stress as well as high response under optimum growing conditions (Keim and Kronstad, 1981; Rajaram et al., 1996). Improving drought tolerance in crops is difficult for the following reasons (Richards, 1996): Drought-resistance mechanisms have been more related to survival mechanisms under drought conditions than to productivity. They are inappropriate to the “normal” target environment and are temporal and, therefore, likely to have minimal impact on growth and yield over the entire lifecycle. Hence, it is important to breed crop varieties that are high yielding stable under non-stress conditions, whilst performing equally well under drought conditions with little yield reduction. Yield stability is important for breeders to adapt varieties to a large number of environments and to furthermore alleviate climate effects, such as less rainfall or higher temperatures.

Yield stability concept can be determined as being dynamic or static (Becker and Leon, 1988). Static concepts assume those genotypes as stable having the same yield independent of environmental effects while dynamic concepts consider those genotypes as stable, which perform close to the general response to the growing conditions. For the selection of high GY, the dynamic concept is most beneficial because genotypes are using optimal environmental resources. The most common approach for examining yield stability is to further partition the genotype by environment (G x E) interaction using an analysis of variance (ANOVA) into linear trends (bi) and a deviation from linear regression (S^2_{di}) (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Becker and Leon, 1988).

Drought tolerance in plants is caused by many different physiological mechanisms (Reynolds and Sawkins, 2005). Three important aspects of drought tolerance are water uptake, water-use efficiency and harvest index (Passioura, 1997). Water uptake is most important for improving the yield potential in drought prone environments, while stable harvest index is associated with higher

yield potential (Blum, 2009; Salekdeh et al., 2009). A further challenge for genotype selection under heavy drought stress conditions is that many important drought related traits generally have lower heritability. Especially those traits, which respond positively under normal years, will be hindered, such as resistance to diseases, tolerance to pre-harvest sprouting and other important objectives. Therefore, an alternating selection in favourable and less favourable conditions facilitates the selection of genotypes that combine both attributes, high yields under stress (water input efficiency) and high yield responsiveness (water input responsiveness) under improved growing conditions but may reduce selection gain (Richards, 1996; Rizza et al., 2004; Kirigwi et al., 2007; Cattivelli et al., 2008).

Much work has been done on several crops to improve drought tolerance and implement genetic resources. Many studies were carried out to detect or improve drought tolerance and implemented genetic resources in different important crops. Several studies deal with wheat (Fischer and Maurer, 1978; Fischer and Sanchez, 1979; Fischer and Wood, 1979; Hoffmann, 2008; Changhai et al., 2010; Fleury et al., 2010; Golabadi et al., 2011), with maize (Bolanos and Edmeades, 1993a; b, 1996; Edmeades et al., 1999; Campos et al., 2004, 2006; Messmer et al., 2009, 2011; Bunce, 2010), with rice (Maclean et al., 2002) and with barley (Thomas et al., 1995; Rizza et al., 2004). The foci of these studies were the semiarid and arid regions of the world, where drought is both regular and intense.

There are different ways to test current breeding material using managed drought stress trials. On the one hand, greenhouse trials or rain-out shelters enable well managed drought stress trials, but are cost and labor intensive and only a small sample of genotypes can be tested (Fay et al., 2000; Yahdjian and Sala, 2002). On the other hand by trials with natural occurring drought stress allow for screening high number of genotypes, but it is not assured that the stress intensity is high enough and that it appears at each test site (Hübner et al., 2013). Direct selection under drought conditions is complicated due to low heritability, polygenic control, epistasis, and significant G x E interaction (Fleury et al., 2010; Golabadi et al., 2011; Weber et al., 2012).

1.3. Quantitative trait loci mapping in rye

The implementation of genetic markers within the last two decades initiated new strategies for plant breeding. Besides identification of heterotic groups and characterization of plant genetic resources, the main focus was to detect monogenic traits and quantitative trait loci (QTL). A lot of work has been done on most major agricultural crops and beyond model organisms, such as *Arabidopsis thaliana*. However, QTL studies in rye lag behind other major agriculture crops. Some QTL studies based on different marker technologies exist. Börner et al. (1999) published the first QTL study based on “Restriction fragment length polymorphism” (RFLP) markers and detected QTL in a F₂ mapping population for different agronomic traits, such as plant height (PH), peduncle length, spike length, and major dwarfing gene *Ddw1*. QTL for plant height were found on chromosomes 2R and 5R (Börner et al., 1999, 2000). QTL for α -amylase activity and connected quality traits have been reported (Masojć and Milczarski, 2005, 2008) and major QTL for TGW were found on chromosome 5R and 7R (Wricke, 2002). High-density maps were constructed after “Single Nucleotide Polymorphisms” (SNP) and “Diversity Arrays Technology” (DArT) became available. Up to now, however, only one genome wide QTL study was published for important agronomic traits within the Petkus gene pool (Miedaner et al., 2012a). QTL for all important traits were described for this intrapool population. QTL for GY, TGW, test weight, falling number, protein, total and soluble pentosan and starch contents were detected. Furthermore in related species, such as triticale (\times *Triticosecale* Wittmack) high affecting QTL were detected on chromosome 5R explaining 42% of genotypic variance for PH and 36% for biomass yield (Alheit et al., 2014), which may represent the dominant rye gene *Ddw1* (Korzun, 1996; Börner et al., 1999; Kalih et al., 2014).

Objectives of this study were to

1. Covariation of grain and biomass yield (Publication I)
 - 1.1. Establish population parameters for experimental interpool hybrids for grain and biomass yield use
 - 1.2. Estimate genetic correlations between grain yield, biomass yield and secondary traits
 - 1.3. Test important agronomic traits for prediction of dry matter yield
2. QTL analysis (Publication II)
 - 2.1. Map QTL for quantitatively inherited traits with a focus on grain and biomass yield and correlated traits
 - 2.2. Constitute the genetic architecture of plant height during growing season
 - 2.3. Detect common QTL for correlated traits
3. Yield stability (Publication III)
 - 3.1. Investigate effects of managed-drought stress on grain yield and heritability
 - 3.2. Evaluate differences in yield stability parameters among three populations with each of 218-220 testcrosses
 - 3.3. Examine the potential of hybrid rye for combining high yield potential with superior yield stability

2. Publication I: Analysis of covariation of grain yield and dry matter yield for breeding dual use hybrid rye

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Abstract

Winter rye (*Secale cereale* L.) becomes more important as substrate for biogas production. This leads to a focus on varieties high yielding in dry matter. In this study, we analyzed the covariation between important agronomic traits for their correlation to dry matter yield and calculated the direct and indirect selection gain for increasing dry matter yield. We tested a set of 258 experimental hybrids for dry matter yield, grain yield and further agronomic important traits at six to eight environments (locations x year combination). We observed a wide range of dry matter yield (10–24 Mg ha⁻¹) and grain yield (6–15 Mg ha⁻¹) among testcross progenies. Genetic variances were significantly ($P < 0.01$) different from zero for all traits. The indirect selection for high dry matter yield using second (EC 51-55) and third (EC 73) plant height measurements was more effective than to using grain yield. Direct selection for dry matter yield was comparable to the indirect selection by the third plant height measurement. Consequently, plant height is a good, non-destructive predictor of dry matter yield, whereas lodging resistance should receive more attention.

3. Publication II: Quantitative-trait loci (QTL) analyses for selection of dual use hybrid rye

3.1. Introduction

Rye (*Secale cereale* L.) is an important cereal crop mainly grown in Central and Eastern Europe. Traditionally, rye is used for baking and feeding, but it became more important for biogas production in the last decade. As genotypic differences for methane yield were negligible, DMY is the most important trait (Hübner et al., 2011). In Germany, hybrid cultivars are most widely used and the importance of hybrids in Austria and Poland is also increasing steadily. Hybrid breeding is successful due to two heterotic groups (Petkus and Carstens pool) and the effective use of a CMS system with pollen-fertilization restoration (Geiger and Miedaner, 1999). Rye is adapted to adverse biotic and abiotic stress factors which allow cultivation on poor soils with deficits in water and nutrients. Therefore, rye is an interesting alternative for biogas production in regions where maize production is not economically viable (Hübner et al., 2011). PH could be used as an indirect trait in order to achieve varieties with high biomass yield (Haffke et al., 2014).

QTL can help to accelerate and alleviate breeding steps for the development of new hybrid rye varieties. Until recently, however, genomics-based breeding was largely unexplored in rye due to missing genomic tools. This has changed with the advent of DArT and SNP genotypic arrays. So far, only one genome-wide QTL analysis has been published for important agronomic traits for testcross progeny of the Petkus gene pool (Miedaner et al., 2012a). One to nine QTL were detected for GY, TGW, test weight, falling number, protein, total and soluble pentosan and starch contents. Total genetic variation explained by QTL ranged from 84% (starch content) to 5% (GY). For all traits, a high G x E interaction was observed. Further, QTL mapping studies exist for individual agronomic traits in rye. For PH, QTL were found on chromosomes 2R and 5R (Börner et al., 1999, 2000). QTL for α -amylase activity and connected quality traits had been reported (Masojć and Milczarski, 2005, 2008). Major QTL for TGW were found on chromosome 5R and

7R (Wricke, 2002). A study on triticale (\times *Triticosecale* Wittmack) detected a major QTL on chromosome 5R explaining 42% of genotypic variance for PH and 36% for biomass yield (Alheit et al., 2014). This QTL seems to represent the dominant rye dwarfing gene *Ddw1* (Korzun, 1996; Börner et al., 1999; Kalih et al., 2014).

The exploitation of high biomass yielding rye hybrid cultivars holds great potential, but until now nothing is known about the genetics of biomass yield in rye. We report the first genome-wide QTL study of an elite interpool (Petkus x Carsten) population for important agronomic traits, including grain and biomass yield. Therefore, our objectives were (1) to identify QTL of quantitatively inherited complex agronomic traits, focused on GY, biomass yield and correlated traits, (2) to identify the genetic architecture for PH through different growth stages and (3) to detect potential colocated QTL for analyzed traits.

3.2. Material and methods

3.2.1. Plant material

A biparental cross between two inbred parents from the Carsten (pollinator) gene pool (H201 and H202) was established by Hybro Saatzucht GmbH & Co. KG and forwarded by single-seed descent to $F_{2:3}$ lines. In total, 258 $F_{2:3}$ lines were crossed with a CMS single cross tester of the Petkus (seed parent) gene pool resulting in 258 three-way hybrids. They were tested along with both testcrossed parents (each parent repeated four times) and the six released hybrid varieties Minello, Visello, Palazzo, Brasetto, SU Drive and SU Stakkato as checks. Plant material development was already described in detail in section I.

3.2.2. Field experiments

Field experiments were conducted in 2011 and 2012 in Hohenheim, Baden Württemberg (48°72'N, 9°20'W), Groß Lüsewitz, Mecklenburg-Western Pomerania (54°07'N, 12°33'W), Wulfsode, Lower Saxony (53°06'N, 10°24'W) and in Bornhof, Brandenburg (53°49'N, 12°89'W). The experiment in Bornhof 2012 failed due to severe pre-summer drought stress. Entries were grown on drilled

plots of 5 to 6 m² size in two experiments grown adjacent to each other: Biomass harvest (exp. 1) and grain harvest (exp. 2). The experimental design within each experiment was a randomized incomplete block design (= alpha design, 34 blocks x 8 entries) with two replications.

For DMY all plots of the first experiment were harvested by a commercial plot chopper at milk ripening (EC 72–77 according to BBCH, exp. 1). The second experiment was harvested with a traditional plot harvester at full ripening (EC 92) for GY. GY is reported as dt ha⁻¹ at 14% moisture and DMY is reported as dt ha⁻¹ and calculated on a 100 % dry matter basis throughout section II. Additional traits recorded for all plots were EG (1–9, 1= very scarce, 9 = very vigorous), HT (1–9, = very early, 9 = very late) SPM and PH at three growth stages (PH 1 at jointing stage EC 32, PH 2 at heading stage EC 51–55 and PH 3 at milk ripening stage EC 73 and before harvest, respectively). These traits were recorded separately for both experiments. For statistical analyses the means of both experiments were calculated as no significant ($P > 0.05$) difference among experiments was found.

3.2.3. Statistical analysis

Statistical analyses were based on plot data of 258 testcross progenies. Checks were calculated separately. All statistical computations were performed with the PLABSTAT software package in a two-step procedure (Utz, 2010). Analyses of variance were firstly performed for all traits in each environment separately. The adjusted entry means from each location were used in a second step to estimate variance components based on the following linear model:

$$y = G + E + G \times E,$$

where G and E denote genotype and environment, respectively. Both factors were treated as random effects. Heritability (h^2) on an entry-mean basis was estimated from the variance components as the ratio of genotypic to phenotypic variance (Fehr, 1987). Simple correlation coefficients (r) were calculated among all traits based on entry means. Significance of r was tested by using tabulated values based on Fischer's z transformation (Fischer, 1921).

3.2.4. Genetic linkage map construction

Genomic DNA was extracted from individual F₂ plants. They were genotyped by SSR and DArT (<http://www.diversityarrays.com>) markers. Polymorphic markers were transformed into genotype codes according to their parental score for the construction of the genetic linkage map. For quality checks a pre-selection with regard to their deviation from expected segregation ratio was performed. The genetic linkage map was constructed with the software JoinMap® 4.1 (van Ooijen, 2006). Based on previously published maps (Bolibok et al., 2007; Milczarski et al., 2011; Miedaner et al., 2012a), we created seven linkage groups concerning the chromosomes (Hackauf, pers. commun.). Genetic distance in centimorgan (cM) and order of each locus were calculated with the maximum likelihood algorithm using Kosambi's mapping function (Kosambi, 1943).

3.2.5. QTL analyses

QTL analyses were based on the genetic linkage map and adjusted entry means using software PLABMQTL (Utz, 2011). Markers with a distance below 1 cM were excluded automatically by the software. Based on testcross performance of F_{2:3} testcross progenies, we can detect the main effect QTL for each trait contributing to the additive-genetic variation. A 1-limit of detection (LOD) support interval was specified around each QTL. Critical LOD thresholds were analyzed empirically for each trait according to Churchill and Doerge (1994) using 2,000 permutation runs. It turned out that critical LOD thresholds corresponding to genome-wide error rates of $\alpha \leq 10\%$ were similar for all agronomic traits. Therefore, the highest LOD threshold (DMY = 3.1) was used for all agronomic traits. The proportion of genetic variance explained by the regression model was calculated as $p_G = R^2_{\text{adj}}/h^2$ where R^2_{adj} is the adjusted proportion of phenotypic variance explained by the model. Additionally, 1,000 cross validation runs were applied to determine the bias of R^2 . For this the data was independently re-sampled 200 times at 5-fold cross-validations (CV). A five-fold CV was performed as follows: The entire data set (DS) was split into five genotypic subsamples, means from four out of five subsamples were used as estimation set (ES) for QTL detection, localization and estimation of genetic

effects. The remaining data group is considered as test set (TS) and was used to conduct a separate QTL analysis. Out of this analysis, we reported the frequency of recovery, i.e. the percentage of validation runs detecting the respective QTL, and the mean QTL effects in ES and TS for comparison.

3.3. Results

Phenotypic data of both parental progenies were similar; testcross progenies represented the mean value of their parents in most instances (Table 4). All traits showed significant ($P < 0.01$) genotypic and G x E interaction variances. The estimates of broad-sense heritability (h^2) ranged from 0.5 for GY and DMY to 0.94 for PH 3. Only SPM had a lower h^2 of 0.35 (Table 4). All traits followed a normal distribution (Figure 3). H202 showed mostly lower values. For HT and TGW both parents had the same values.

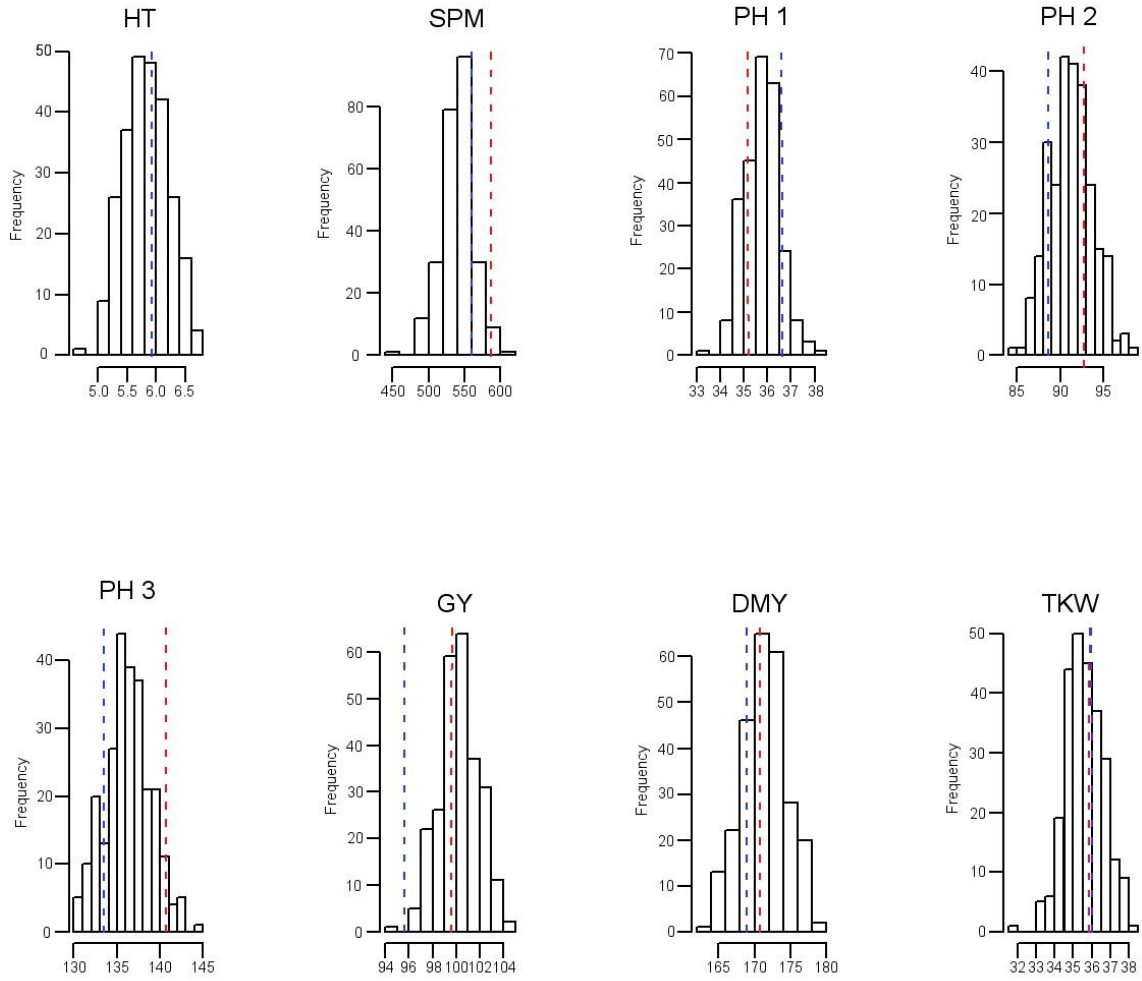


Figure 1. Normal distribution of all eight traits. Dashed lines mark means of parents (red = H201, blue =H202)

Coefficients of phenotypic correlation were significant ($P < 0.05$) among most traits (Haffke et al., 2014). GY and DMY were significantly positively correlated ($P < 0.01$) to all other seven traits with the exception of the correlation between GY and EG ($P < 0.05$) and no correlation between DMY and SPM. The correlation between DMY and GY was moderate ($r = 0.33$, $P < 0.01$). Highest correlation was observed between PH 2 and PH 3 ($r = 0.76$, $P < 0.01$), followed by PH 2 to DMY ($r = 0.64$, $P < 0.01$) and PH 3 to DMY ($r = 0.52$, $P < 0.01$). Detailed data on these correlations has recently been published (Haffke et al. 2014).

Table 1. Means of two parental progenies (H201, H202) and means, ranges, estimates of variance components (genotypic, σ_G ; genotype x environment interactions, $\sigma_{G \times E}$; and pooled error σ_e), heritabilities h^2 , least significant difference at $P < 0.05$ (LSD 5%) for both dry matter yield (DMY) (exp. 1) and grain yield (GY) (exp. 2) as well as secondary traits^a of 258 testcross (TC) progenies evaluated across seven environments.

Material	Parameter ^a	HT (1-9) ^c	SPM ^b	PH 1 ^b (cm)	PH 2 (cm)	PH 3 (cm)	TGW (g)	GY (dt ha ⁻¹)	DMY (dt ha ⁻¹)
H201		5.93	586.84	35.16	92.79	140.67	35.89	99.66	170.78
H202		5.93	559.93	36.60	88.56	133.42	35.98	95.60	168.84
Parental							35.94		
Mean		5.93	573.39	35.88	90.68	137.05		97.63	169.81
TC-Population	MEAN	5.83	540.46	35.77	91.2	136.29	35.61	100.28	171.44
	MIN	4.79	285.88	33.34	84.95	130.25	38.45	94.28	163.57
	MAX	6.79	893.29	38.25	98.54	144.11	31.85	104.24	179.64
	LSD _{5%}	0.61	50.22	1.00	1.98	1.73	0.95	3.23	6.23
	σ_G	0.10**	172.97**	0.42**	5.49**	6.68**	0.89**	1.48**	4.75**
	$\sigma_{G \times E}$	0.17**	242.00**	0.23**	1.87**	0.81**	0.27**	3.78**	10.14**
	σ_e	0.34	1724.09	1.1	3.42	3.82	0.43	5.71	25.15
	h^2	0.67	0.35	0.76	0.92	0.94	0.88	0.52	0.49

** Significant at 0.01 level of probability,

^a HT, heading time; SPM, spikes per square meter; PH 1-3, plant height measured in EC 32, EC51-55 and before harvest, respectively, GY, grain yield; DMY, dry matter yield, ^b Results based on six environments, ^c HT: 1 = very early, 9 = very late.

The genetic linkage map comprised a total length of 964 cM with an average marker density of 1.06 cM. The seven rye chromosomes had a total length ranging 105 to 166 cM. The majority of markers had a distance of less than 1 cM. In total, 43 QTL were detected with a LOD threshold ≥ 3.10 (Table 5). Most QTL were found for TGW (10) and HT (7), for SPM only one QTL was significant. The explained genotypic variance of individual QTL ranged from 3% to 46%. Explained genotypic variance for HT with all seven detected QTL simultaneously reached 85%. For the other traits, this estimate ranged from 42% for SPM to 81% for PH 3. Several major QTL ($P_G \geq 20\%$) were detected for HT, SPM, PH 2, PH 3, GY, and DMY. Interestingly, two major QTL for DMY and PH were found in the same positions on chromosomes 2R and 5R (Figure 4, Supplementary-Table S1). A large QTL for GY ($P_G = 40\%$) was also detected on chromosome 2R about 20 cM apart (Figure 4).

3.4. Discussion

In this study we analyzed an elite testcross population of 258 lines to reveal the genetic architecture of eight important agronomic traits in hybrid rye. Phenotypic data were collected on each of four locations in 2011 and 2012, excluding Bornhof in 2012. We observed significant genetic variation ($P < 0.01$) for all traits. Heritabilities ranged from 0.35 to 0.94. For the three PH measurements (PH 1, PH 2, PH 3) we observed the highest heritabilities (0.76, 0.92, 0.94, respectively), which agrees with other results in rye (Miedaner et al., 2010, 2012b). For GY and DMY we obtained moderate heritabilities of 0.52 and 0.49, respectively. In both biparental populations of the Petkus gene pool, the heritability estimates for grain yield are slightly higher (0.70)(Miedaner et al., 2012a). Similar results were obtained for triticale (ranging from 0.77 – 0.91) and barley (ranging from 0.72 – 0.92), while results for wheat was comparable to our results (ranging from 0.41 – 0.58) (Mühleisen et al., 2014). The parental mean did not differ from progeny mean in all traits, except for HT and TGW, indicating a predominantly additive inheritance.

The use of DArT makers resulted in a map with a total length of 964 cM and average an marker density of 1.06 cM that is comparable to other studies in rye

(Bolibok et al., 2007; Milczarski et al., 2011) and one population of the Petkus gene pool (Miedaner et al., 2012a). The genetic map of the other population of the Petkus gene pool resulted in much longer chromosomes, but results are comparable because of several identical makers (Miedaner et al., 2012a). For QTL studies, marker distances of 15–20 cM are adequate (Piepho, 2000). Therefore, we consider QTL that are closer linked than 20 cM as having the same chromosomal position.

Table 2. Number of QTL for all eight traits. R^2_{total} and R^2_{CV} (based on 1000 cross validations) for each trait and common QTL with GY and DMY.

Trait	QTL	R^2_{total}	R^2_{CV}	Common QTL	
				GY	DMY
HT	7	56.72	41.70	1	1
SPM	1	15.39	7.12	0	0
PH 1	4	31.86	19.56	0	0
PH 2	2	55.22	51.71	1	2
PH 3	12	76.12	61.00	0	0
GY	3	34.12	23.89	-	0
DMY	3	23.27	10.32	0	-
TGW	10	61.79	38.47	1	0

HT, heading time; SPM, spikes per square meter; PH 1-3, plant height measured in EC 32, EC51-55 and before harvest, respectively, GY, grain yield; DMY, dry matter yield,

3.4.1. QTL for agronomic traits

One to twelve QTL were found for the eight traits in this population. The lowest number was revealed for SPM, having also the lowest heritability and DMY. The total proportion of explained phenotypic variance ranged from 41% for SPM to 85% for TGW. Most QTL were found for HT, TGW and PH 3. For HT, seven QTL were segregating the population, explaining in total 85% of the genetic variance. The highest effect (20.4%) was found on the short arm of chromosome 7R. For TGW even 10 QTL were detected with 70% of explained genotypic variance. Similarly, four to six QTL for TGW were detected in two rye populations by Miedaner et al. (2012). In their study, one QTL with a high effect (40.5%) on chromosome 7R (long arm) was found. Therefore it could be a new described QTL

or belong to one of the major QTL, which were already described (Wricke, 2002). Comparison of QTL positions in detail is possible in general, but both studies provide only a few common markers although both were constructed with about 1,000 DArT markers (Miedaner et al., 2012a).

For PH, we found a total of 11 QTL over all three developmental stages. All detected QTLs for PH 1-3 were dynamic during plant growth except for one QTL (chromosome 2R, position 85 – 88), which was found in developing stages PH 2 and PH3. This indicates that most of the detected QTLs controlling PH are highly dynamic, which is consistent with the theory of developmental genetics that several genes control the same quantitative trait and are expressed at different development stages. Our findings agree well with results in other crops. In maize, eight dynamic QTL were described while only three QTL were commonly detected during subsequent developing stages (Yan, 2003). Analogous results were described in rice (Yan et al., 1998; Cao et al., 2001) and wheat (Zhang et al., 2013). A QTL for GY ($P_G = 12.8\%$) was co-localized with a QTL for TGW (3.2%) on chromosome 5RL, however, the effect of the TGW-QTL was small. Most QTL underlined a significant QTL x environment interaction. This is typical for quantitative traits and makes selection more difficult. To report only those QTL that surmount the threshold across seven environments may have also contributed to a low number of QTL per trait. However, only environmentally stable QTL are useful for breeding.

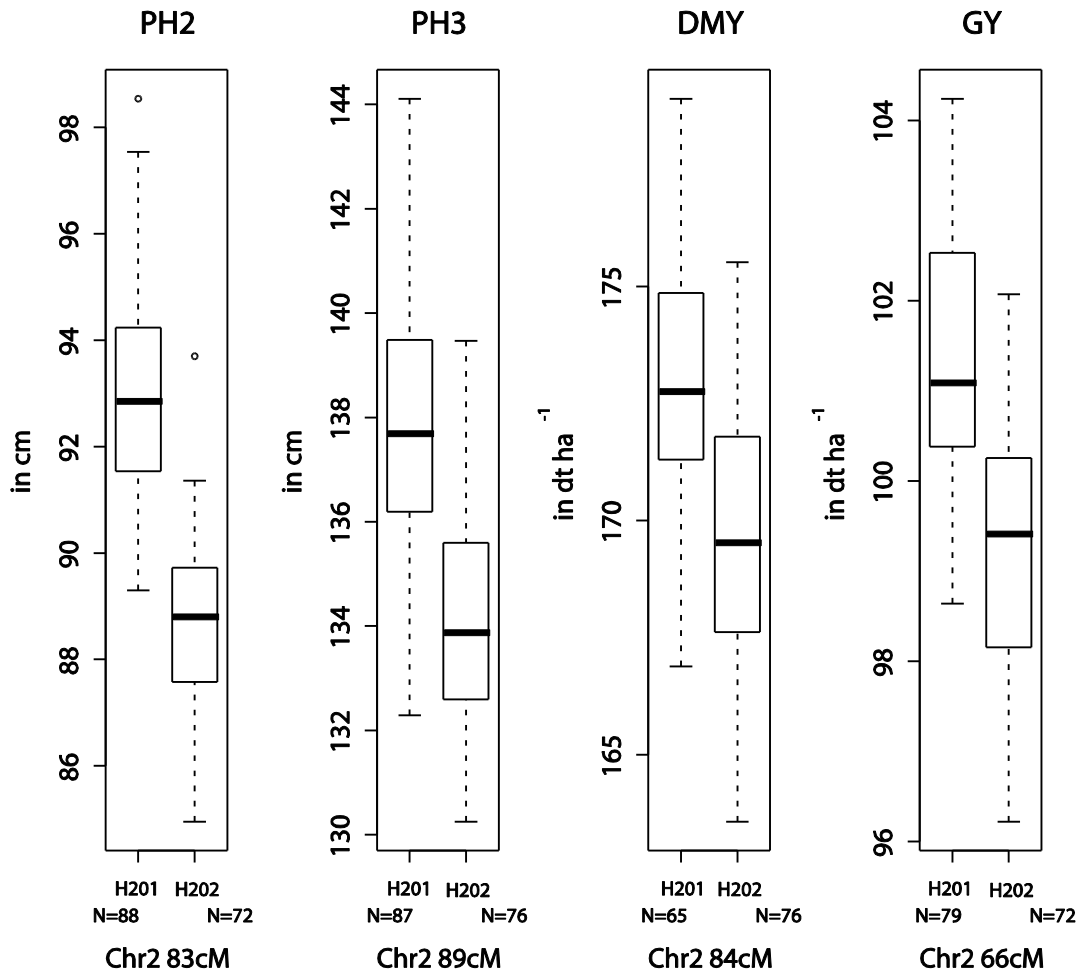


Figure 2. Effects of alleles from parent 1 (H201) and 2 (H202), respectively, for plant height (PH) at two assessment dates (2,3), dry matter yield (DMY), and grain yield (GY) on chromosome 2R and positions given in centimorgan (cM).

3.4.2. Grain yield QTL with high effect

It is known that grain yield is a complex trait and affected by a multitude of QTL. Miedaner et al. (2012) found in population seven QTL which explained a genetic variance from 10 to 24% (in total 81.8%). In contrast to this, we found only three QTL for GY in total, one QTL explained 40% of genotypic variance. In other crops high effect QTL for GY were described as well: For rice, a QTL with phenotypic effects under drought stress of 51% (Bernier et al., 2007, 2009), 58% (Venuprasad et al., 2011) and 31% (Venuprasad et al., 2009) were reported.

QTL for grain yield with similarly high effects were found for maize. Phenotypic variance of 47.2% were explained by one QTL found under different water regimes (Tuberosa et al., 2002b). Further, different studies detected high-effect QTL for GY in wheat. Kiriwi et al (2007) described three single QTL for GY (each

explained of 15–20% R^2) and DMY (each explained of 29–32% R^2) located on the same chromosomal positions. High effect QTL for GY with R^2 ranging from 15%–34% were described in recombinant inbred lines of wheat (Rustgi et al., 2013).

Furthermore, the fact that the plant material was based on current breeding material for high yielding hybrid varieties may have an influence on the genetic architecture and therefore, an effect of single QTL with high effects. Consequently, further research is needed to investigate the genetic analysis of QTL for complex traits in rye.

3.4.3. Plant height and heading time are components of biomass yield

A significant positive correlation between DMY and PH 2 ($r = 0.64$) has been found in this hybrid rye population (Haffke et al., 2014). It is known that QTL of correlated traits often map together. In fact two QTL for DMY (42.56%) and two QTL for PH 2 (60.02%) were found at the same position on chromosome 2R and 5R. The frequency of recovery in CV for both QTL was higher for PH (94% and 92%) than for DMY (44% and 71%).

PH is obviously an important component of biomass yield. PH is inherited either by single dwarfing loci with high effects, that have been extensively used in wheat (Worland et al., 1998; Korzun et al., 1998), barley (Wang et al., 2010; Vu et al., 2010; Chandler and Harding, 2013), and triticale (Oettler, 2005) or by a large array of QTL each with small effects. An analysis of an introgression library with primitive rye, a likely progenitor of cultivated rye, showed that 59 out of 72 lines had chromosomal segments increasing PH in *per se* performance (Miedaner et al., 2010). In this study, we also found 18 QTL responsible for PH 1–3 with proportions of explained genotypic variance ranging from 3 to 16% and one QTL on chromosome 2 with even 46%. Because heritability was high, this QTL still explained 42% of phenotypic variance. The same locus (or a cluster of linked loci) on chromosome 2R also reduced biomass yield (-1.6 dt ha^{-1}) and made the progenies later in heading time (Figure 4). The effects of this QTL were large with the allele from parent H202 reducing PH 2 by 4.32 cm, PH 3 by 3.76 cm and DMY by 3.32 dt ha^{-1} . Indeed, Börner et al. (1996) described a dwarfing gene on

chromosome 2R (*dw2*) in the centromeric region. However, this gene is inherited recessively and thus, no candidate for the large-effect QTL is described here. Similarly, Alheit et al. (2013) found a QTL with high effect on plant height (-11,4 cm) in triticale, which considerably reduces biomass yield (-14.4 dt ha⁻¹), most likely representing the dominant rye dwarfing gene *Ddw 1* (Kalih et al., 2014). Obviously, height-reducing genes for QTL are counterproductive for maximizing biomass yield. QTL on chromosome 2R also affecting HT illustrates that earlier progenies tended to have higher biomass. This was also obvious when tested in testcrosses with rye germplasm resources (Miedaner et al., 2010), where significant correlations between EG and DMY were reported.

Another QTL affecting several traits in parallel is located on chromosome 5RL. The allele of parent H201 resulted in earlier (HT), taller (PH 1–2) progeny with higher DMY. However, effects and recovery frequencies in the CV of the QTL on chromosome 5RL were smaller. A QTL for GY is located in vicinity of this QTL on 5R.

3.4.4. Conclusions for breeding dual use hybrid rye

Selection for short-strawed progenies is a common goal among rye breeders to achieve higher lodging resistance (Geiger and Miedaner, 2009). However the selection cannot be as strong as in wheat because the stem plays a larger role in contributing assimilates to the head compared to wheat. Selection for high biomass yield affords a new course in this breeding goal.

For GY and DMY we detected no common QTL. However, both QTL for DMY on chromosomes 2R and 5R were in vicinity of two QTL for GY with a distance of 17 and 20 cM, respectively. Given the high error of chromosomal localization of QTL (Utz et al., 2000), this might still represent the same locus. On the other hand, we found only a low correlation of GY vs. DMY ($r = 0.33$, Haffke et al. 2014). This could be a hint, that either the QTL are different for both traits or that more co-localized QTL for both traits are available in this population that could not be mapped due to gaps in the genetic map (e.g. on chromosome 3R), QTL x environment interaction or by the fact that some QTL are not exceeding the

threshold. However, the low genotypic correlation between GY and DMY supports the first explanation. In contrast, higher correlations between GY and DMY were found in barley ($r = 0.76$, Boukerro et al. 1990), triticale ($r = 0.65$, Gowda et al. 2010) and wheat under drought stress ($r = 0.77$ (Leilah and Al-Khateeb, 2005) and $r = 0.69$ (Saleem, 2003)). That will lead to a focus on two main breeding goals in hybrid rye breeding programs. On the one hand, classical breeding goals as GY, TGW, short straw, and further quality traits have to be followed, on the other, hand maximal DMY must be considered.

We already suggested selecting high biomass yielding varieties by indirect selection on PH (Haffke et al. 2014). On the other hand, yield tallness is an excellent indirect selection criterion for improving biomass, yielding a higher indirect selection gain than the direct selection on DMY (Haffke et al. 2014). This conclusion is supported by our QTL results. The old Polish cultivar Danko is a perfect example of a genotype with superior lodging resistance despite tallness.

Because the correlation between GY and DMY is not negative, hybrids for dual use can be achieved (Haffke et al., 2014). However, they have to be tested for both traits separately. In a multistep approach, GY could be selected in the first test for combining ability and subsequently DMY in the next test among the GY-selected progenies. When PH is already considered in the first test, an indirect selection gain for DMY can already be exploited. In future, genomic selection should make it easier to select for contrasting traits in the same run. Selection in high biomass should result in higher gains because lower traits have to be considered. Caused by the previously explained greater genetic variance and higher recovery frequency of CV for PH QTL it is superior to select indirectly by MAS on high biomass yielding varieties by avoiding height reducing QTL alleles like the prominent PH QTL on chromosome 2R and favoring height inducing QTL like that on chromosome 5R. When selecting for taller plants to increase biomass yield it is important to focus on better lodging resistance.

3.5. Supplementary tables

Table S1. Quantitative trait loci (QTL) of eight agronomic traits based on 10% LOD threshold at 3.10 (based on 2,000 permutation test) and a 1,000 cross-validation for Pop-D.

Trait	QTL	Chr.	Pos	SIL	SIR	Left-Marker	Right-Marker	LOD	Effect ^a	P _G ^b	QTL x E ^d	Freq. CV ^c	EffectES ^e	EffectTS ^f
Heading time	$\Sigma 7$							$\Sigma 84.65$						
	QHdt-2R.1	2R	69	68	70	XrPt-507619	XrPt-508957	6.304	-0,133	8,6	**	0.9000	-0.188	-0.205
	QHdt-2R.2	2R	86	83	88	XrPt-509592	XrPt-402599	5.313	-0,173	15,33	**	0.7470	-0.166	-0.143
	QHdt-4R.1	4R	6	0	14	XtPt-3302	XrPt-507297	5.882	0,109	9,5	**	0.7190	0.121	0.108
	QHdt-4R.2	4R	69	67	70	XrPt-509132	Xtc368556g	6.868	0,103	8,76	**	0.3560	0.108	0.069
	QHdt-5R	5R	105	99	108	Xtcos1359	XrPt-400590	4.351	0,139	14,45	**	0.5570	0.145	0.121
	QHdt-6R	6R	9	7	10	Xtnac1727	XrPt-5403	4.477	0,105	7,57	**	0.3470	0.118	0.071
	QHdt-7R	7R	57	56	59	XrPt-402149_r	XrPt-399686	10.322	-0,165	20,44	**	0.8200	-0.152	-0.140
Spikes per m ²	$\Sigma 2$							$\Sigma 43.98$						
	QSsm-3R	3R	70	69	72	Xscm239-3R	XrPT-507655	3.470	-9.699	23.52		0.2550	-10.621	-8.185
	QSsm-5R	5R	49	48	52	XtPT-3980	Xtcos5220-5RL	3.807	9.267	20.46		0.3550	9.780	7.969
Plant height (cm) 1	$\Sigma 4$							$\Sigma 41.92$						
	QPh1-2R	2R	26	22	28	XrPt-389385	XrPt-399784	6.025	0.213	6.37		0.4560	0.233	0.156
	QPh1-4R	4R	41	37	43	Xscm352	XrPt-400363_r	3.404	0.312	10.69		0.3980	0.322	0.256
	QPh1-5R	5R	92	90	96	XrPt-389427	Xtnac1454	10.274	0.405	15.57		0.9230	0.392	0.367
	QPh1-7R	7R	57	56	60	XrPt-402149_r	XrPt-399686	9.624	-0.285	9.29		0.9600	-0.307	-0.296

Table S1 continued

Trait	QTL	Chr.	Pos	SIL	SIR	Left-Marker	Right-Marker	LOD	Effect ^a	P _G ^b	QTL x E ^d	Freq. CV ^c	EffectES ^e	EffectTS ^f
Plant height (cm) 2	Σ 2				Σ 60.02									
	QPh2-2R	2R	85	83	86	XrPt-508452	XrPt-509592	44.584	-2.136	45,77	**	0,941	-2.011	-2.074
	QPh2-5R	5R	106	104	108	Xtcos1359	XrPt-400590	12.814	1.051	14,25	**	0,915	1.037	1.027
Plant height (cm) 3	Σ 12				Σ 80.98									
	QPh3-2R.1	2R	8	3	10	XrPt-401176	XwPt-345417	4.341	0.508	3.06	-	0.2410	0.526	0.323
	QPh3-2R.2	2R	55	54	57	XrPt-509223	Xscm23	7.006	-0.785	4.90	-	0.4250	-0.730	-0.554
	QPh3-2R.3	2R	88	87	90	XrPt-402599	Xtcos5085-2RL	17.008	-1.506	12.91	**	0.9730	-1.622	-1.774
	QPh3-2R.4	2R	118	112	122	XrPt-390369	XrPt-505385	9.574	-0.889	5.82	-	0.9250	-0.812	-0.724
	QPh3-3R	3R	49	47	51	Xscm84-3R	Xscm87-3R	18.783	1.191	11.04	**	0.9150	1.196	1.146
	QPh3-4R.1	4R	4	0	11	XtPT-3302	XrPt-507297	6.513	-0.686	4.72	**	0.7240	-0.683	-0.603
	QPh3-4R.2	4R	51	49	53	XrPt-400488	Xscm356	20.772	-1.186	12.28	-	0.9470	-1.076	-1.043
	QPh3-5R.1	5R	68	66	70	XrPt-401067_r	Xtcos4572	3.116	-1.117	10.34	-	0.6590	-1.126	-1.033
	QPh3-5R.2	5R	141	137	142	Xtcos996-5RL	Xscm365-5R	5.428	0.644	4.20	**	0.6490	0.696	0.630
	QPh3-6R.2	6R	41	39	42	XrPt-506526	XrPt-411297	5.527	-0.611	4.01	-	0.2800	-0.658	-0.513
	QPh3-6R.2	6R	84	82	86	XrPt-506099	XrPt-399884	8.125	0.772	5.45	-	0.5240	0.733	0.507
	QPh3-7R	7R	47	45	54	Xtcos1958_7RS	XrPt-389653_r	4.078	0.440	2.25	-	0.3510	0.558	0.283
Grain yield (dt ha ⁻¹)	Σ 3				Σ 65.63									
	QGyd-2R	2R	66	64	69	Xscm188	XrPt-508470	18,8	-1,16	40,21	**	0,914	-1.127	-1.087
	QGyd-3R	3R	81	75	83	XrPt-401113	XrPt-398525	5,34	-0,55	12,66	-	0,254	-0,565	-0,429
	QGyd-5R	5R	126	124	128	Xtnac1388-5R	Xtcos3096-5R	4.926	0,608	12,76	*	0,599	0,634	0,438

Table S1 continued

Trait	QTL	Chr.	Pos	SIL	SIR	Left-Marker	Right-Marker	LOD	Effect ^a	P _G ^b	QTL x E ^d	Freq. CV ^c	EffectES ^e	EffectTS ^f
Dry matter yield (dt ha ⁻¹)	Σ 3									Σ 47.49				
	QDmy-2R	2R	83	81	86	XrPt-508452	XrPt-509592	4.954	-1.445	24.80		0.5000	-1.553	-1.384
	QDmy-3R	3R	50	46	52	Xscm87-3R	XrPT-401504	3.362	0.951	8.91		0.2690	1.128	0.492
	QDmy-5R	5R	106	97	108	Xtcos1359	XrPt-400590	3.389	1.199	13.78	**	0.5580	1.176	0.814
1000-grain weight (g)	Σ 10									Σ 70.21				
	QTgw-1R.1	1R	69	67	70	XrPt-505603	XrPt-400866_r	18.485	0,545	14,68	-	0,664	0,536	0,516
	QTgw-1R.2	1R	133	130	138	Xscm171	XrPt-507839	4.406	0,205	2,77	-	0,174	0,268	0,116
	QTgw-2R	2R	106	104	107	XrPt-505455	XrPt-398612_r	4.399	-0,591	17,34	-	0,141	-0,522	-0,485
	QTgw-3R	3R	45	39	47	XrPt-506847	Xscm84-3R	4.816	0,277	4,24	-	0,15	0,298	0,137
	QTgw-4R.1	4R	31	25	36	XrPt-400085_r	Xscm352	5.236	-0,297	2,57	**	0,197	-0,413	-0,246
	QTgw-4R.2	4R	51	50	52	XrPt-400488	Xscm356	13.376	-0,536	7,24	-	0,616	-0,647	-0,634
	QTgw-4R.3	4R	69	68	70	XrPt-509132	Xtc368556g	6.737	0,563	10,41	-	0,561	0,569	0,539
	QTgw-5R	5R	119	118	125	Xtnac1394	XrPt-506735	6.512	0,222	3,21	-	0,124	0,275	0,111
	QTgw-6R	6R	2	1	4	XrPt-508161	XrPt-399992	4.183	-0,234	3,4	-	0,096	-0,29	-0,132
	QTgw-7R	7R	5	4	7	XrPt-508123	XrPt-507064_r	4.311	0,242	4,35	-	0,413	0,262	0,166

QTL, quantitative trait loci; Chr, chromosom; Pos, position in cM; SIL, Support intervall left in cM; SIR, support intervall reight in cM; Left-M, left Marker; Reight-M, reight Marker; LOD, critical LOD value,

^a Additive effect, ^b part of the explained genetic variance, ^c Frequency in cross-validation, ^d QTL by environment interaction tested for significance (sequentially rejective Bonferroni F-test), ^e mean QTL effect in the estimation sets of cross-validation, ^d mean QTL effect in the test sets of cross-validation

4. Publication III: Yield stability of hybrid rye under normal and managed drought stress conditions towards selection of broadly adapted germplasm

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Abstract

Extreme weather events, induced by global climate change, will affect crop production and create a demand for ecologically stable and high-yielding varieties. Winter rye (*Secale cereale* L.) is mainly grown in marginal environments in Central and Eastern Europe, where varying weather conditions have an even stronger impact on grain yield. Therefore yield stability is an important breeding goal. Our objectives were to describe phenotypic diversity for genotype by irrigation interaction (GII) under managed drought stress and to analyze the possibility of combining high grain yield and maximal yield stability of hybrid rye. We observed two intrapool (each of 220 testcross progenies) and one interpool (218 testcross progenies) population at 16 to 18 environments (location by year combination), while managed drought stress trials were conducted at six of these environments. We observed a wide range of grain yield, from 4.9 to 11.5 Mg ha⁻¹. In the managed drought-stress experiments yield reduction in the rainfed regime ranged from 2 to 41% with an average of 18%. In most environments yield reduction was significant, while only a few environments showed significant GII. High genotypic correlations between irrigated and rainfed regimes (0.8–1.0) indicate already stable hybrid rye genotypes under differing water conditions. The coefficient of linear regression (b_i) was not significantly different from 1 among progenies. Mean square deviation from linear regression (S^2_{di}), however, varied significantly ($P < 0.01$). Although modern rye breeding materials show already high yield potential and stability, it is proposed to include managed drought stress environments in selection process to ensure a broad adaptability in future.

5. General discussion

Increasing GY or biomass yield is still the main aim in breeding programs. The future challenge for all breeding programs will be to deal with global climate change. Furthermore, biotic and abiotic stresses will have a much stronger impact on our cultivated agriculture crops. Therefore, stable and high yielding varieties are needed. In this study, we evaluated four different interpool and intrapool testcross hybrid rye populations (Table 9).

Table 3. Detail information about all evaluated populations.

Population	Pop-A	Pop-B	Pop-C	Pop-D
Developed by	KWS	KWS	KWS	HYBRO
Population type	Intrapool	Intrapool	Interpool	Interpool
Testcross progenies	220	220	218	258
Environments ^a (total)	16	16	18	7
Environments ^a (irrigated vs. rainfed)	6	6	6	-
Section	III	III	III	I, II
Main trait	GY	GY	GY	DMY, GY

^a Location x year combinations are called environments

KWS= KWS Cereal GmbH; HYBRO = HYBRO Saatzucht GmbH & Co. KG;

GY = Grain yield, DMY = Dry matter yield;

The intrapool populations Pop-A and Pop-B were based on three parental elite inbred lines from the Petkus (seed parent) gene pool and were connected through one identical parent. All lines of Pop-A and Pop-B were crossed to an unrelated CMS single cross tester of the Petkus gene pool resulting in three-way intrapool crosses and evaluated together with their testcrossed parents. The interpool populations, Pop-C and Pop-D, are based on biparental crosses between two inbred parents from the Carsten (pollinator) gene pool and crossed with a CMS single cross tester of the Petkus (seed parent) gene pool by open pollination. Both populations were not connected to each other and developed independently.

5.1. QTL analysis on grain and biomass yield

Due to the increasing demand for renewable energy produced using plant biomass, high biomass yielding rye varieties have become more important in agricultural production systems. Recently, it was demonstrated that different sources of rye germplasm possess a great potential for improving biomass yield production (Miedaner et al., 2010) and therefore, increasing the amount of energy produced per hectare. Although hybrid rye has a high potential as a bioenergy crop and shows large DMVs, methane yield per hectare is the most important trait for economic biogas production. Therefore, when using hybrid rye as a bioenergy resource for biogas production, high DMV is the most important trait. DMV and methane yield were highly correlated ($r = 0.95$, $P < 0.01$), while harvest time only had an influence on DMV and was highest during harvest at late milk ripening (Hübner et al., 2011). Similar correlations ($r = 0.90$) between DMV and methane yield were reported for maize (Grieder et al., 2012b). Different hybrid rye varieties have been released within the last years, which could be used for both production schemes - GY or DMV.

We analyzed Pop-D at four locations in 2011 and 2012 and phenotypic data were collected for important agronomic traits. Further, we calculated a linkage map based on approximately 1200 SSR and DArT markers. Phenotypic results pointed out that a simultaneous selection for GY and DMV is not adequate due to the rather low correlation between both traits. For a successful indirect selection, genetic correlation coefficients of >0.65 should exist between the trait of interest and the trait for selection (Harrer and Utz, 1990). The highest genetic correlations to DMV were observed for PH 2 and 3 ($r = 0.89$, and $r = 0.89$, respectively). The stem had a higher influence on DMV than the ear. Due to high correlation and high heritability of PH, it is more efficient to select indirectly for high DMV by using PH. Furthermore, an indirect selection of DMV using GY or vice versa would not be advisable and would lead to a low response to selection due to the low phenotypic correlation between these traits with only $r = 0.33$ in our study (see section I). The relative efficiencies for selection of DMV estimated by PH 2 and PH 3 were 1.24 and 0.98 respectively, compared to 0.52 for GY

(Haffke et al., 2014). In contrast to this, higher correlations between GY and DMY were found for barley $r = 0.76$ (Boukerrou and Rasmusson, 1990) and triticale $r = 0.65$ (Gowda et al., 2011). Gowda et al. (2011) used an index of traits to predict the biomass yield. Generally, PH can be considered as a good proxy for biomass production (here DMY). High correlation between PH and DMY ranging from $r = 0.64$ to $r = 0.81$ were found in maize (Lübberstedt et al., 1997; Strigens et al., 2012; Grieder et al., 2012a; b), $r = 0.68 - 0.70$ in sorghum (Murray et al., 2008) and slightly higher correlations of $r = 0.86$ in triticale (Alheit et al., 2014).

The genetic results were in agreement with our phenotypic results, because similar QTL for PH and DMY were obtained, while no overlapping QTL between GY and DMY were found. QTL for PH and DMY were co-localized on chromosome 2R and 5R with R^2 of 60.0% and 42.9%, respectively. Co-localized QTL for PH and DMY were also reported in maize (Lübberstedt et al., 1997). Due to its high correlation, higher heritability and higher relative selection efficiencies as mentioned above focusing on PH for improving high dry matter yielding varieties is more successful.

To achieve high yielding biomass rye populations it will be necessary to focus on taller plants (Salas Fernandez et al., 2009). This is contrary to classical breeding targets, which aim at short plant types with high GY. Traditional aims were to develop short, lodging tolerant and high grain yielding varieties which were adapted to the mechanical harvest (Sakamoto and Matsuoka, 2004; Geiger and Miedaner, 2009). New breeding aims for high biomass yielding varieties should mainly focus on increased PH in order to exploit the positive correlation with DMY. This goes along with a different harvest index. Modern varieties of most intensively cultivated grain crops have a harvest index range between 0.4 and 0.6, when focusing on high grain yielding varieties. An altered harvest index can have a positive influence on high yielding biomass varieties.

In order to achieve high biomass yielding hybrid varieties, selection within the two gene pools is necessary. Breeders should focus on line *per se* performance evaluation on PH and DMY. Moderate to high phenotypic correlations were found

for two rye populations between line *per se* and testcross performance for PH of $r = 0.40$ and $r = 0.70$, respectively (Miedaner et al., 2014).

A further opportunity would be the use of genetic resources (Haussmann et al., 2004). Within germplasm resources for forage rye and grain rye high phenotypic correlations of $r = 0.60$, $r = 0.84$ and $r = 0.79$ between line *per se* and testcross performance for PH were found, respectively (Miedaner et al., 2010). Additionally, high correlations ($r = 0.70$) were obtained for forage rye between line *per se* and testcross performance for DMY. Also phenotypic correlation of PH and methane yield between line *per se* and testcross performance of $r = 0.61$ was reported in maize (Grieder et al., 2012a).

Since tall genotypes can often be found in exotic genetic resources, one opportunity to improve both, PH and DMY, could be achieved by exploiting these resources. A few putative QTL for PH were already described in Iranian primitive rye populations and could be introgressed into high yielding modern rye genotypes (Falke et al., 2009a; b; Miedaner et al., 2011). Nevertheless, using genetic resources bears further obstacles, since these genotypes possess mostly very poor agronomic performance and might lead to genomic distortions due to their genetic distance compared to our current rye breeding pools (Haussmann et al., 2004).

An increase in DMY in hybrid rye varieties by increasing PH needs better lodging resistance. Generally better lodging tolerance is highly correlated to short varieties and has been reported for rye (Oehme, 1989), barley (Stanca et al., 1979; Murthy and Rao, 1980) and wheat (Pinthus, 1967) to achieve a favorable harvest index and, hence higher GY for biomass rye breeding. It is therefore, necessary to evaluate other agronomic traits, which might improve lodging resistance apart from PH reduction. Several possibilities were described in other crops to improve lodging resistance besides using PH. In wheat, the spreading angle of roots in a horizontal direction was positively correlated to lodging tolerance (Pinthus, 1967). Further, the culm stiffness (Keller et al., 1999) and thicker and heavier stems may lead to less lodging in varieties (Zuber et al., 1999). In Sorghum larger diameters of basal internodes, a thicker rind, higher

total non-structural carbohydrates and lower stalk potassium and protein concentrations lead to more lodging tolerant varieties (Esechie et al., 1977). QTL for lodging resistance in rice (Kashiwagi and Ishimaru, 2004) and wheat (Keller et al., 1999) have already been described.

5.2. Improving yield stability and drought tolerance in hybrid rye

Released varieties are destined for a wide range of environments. Equally as important as different breeding aims, such as high GY or DMY, is the importance of breeding for stable varieties over a wide range of environments and different years (Kang and Magari, 1996).

Rye is grown in various agroecological zones under different soil conditions. It is mainly grown in Northern Europe stretching from Germany to the Ural Mountains in the east, covering a range of continental to oceanic climate conditions. Such a wide range of environmental conditions poses a great challenge to rye breeders. In order to set up an efficient breeding program with maximum response to selection, breeders need to define target environments based on G x E interactions and exemplary geographical regions, weather events and growing conditions. Estimating and understanding the extent of G x E interaction can guide breeders in their decision on whether a breeding strategy for either specific or wide adaptation should be pursued, which depends on the expression of stability under limited or wide ranges of environments (Romagosa and Fox, 1993; Yue et al., 1997). Generally, breeding for widely adapted genotypes would be an advantage, but the question is how broadly new varieties should be adapted (Ceccarelli, 1989). Ceccarelli (1989) suggested two different approaches for success. On the one hand, one could select for low G x E interaction and high yield. On the other hand, one could select for maximum yield and stability within macro-environments. Subdivided target environments have also been suggested (Atlin et al., 2000). Generally, hybrids have been reported to be more stable across environments than inbred lines as shown for several auto- and allogameous crops (Lewis, 1954; Adams and Shank, 1959; Shank and Adams, 1960; Allard, 1961; Becker et al., 1982; Mühleisen et al., 2014). Individual and collective buffering is part of the genetic structure and

heterozygous and heterogeneous types in rye provide both. The heterozygosity of most loci causes individual buffering while segregation of loci within the variety causes the collective buffering. The advantages of heterogeneous crops increases, when water and nutrient increases (Frey and Maldonado, 1967). Therefore, hybrid rye should already be highly stable and genetically flexible (Phillips and Wolfe, 2005).

We tested 658 rye genotypes from three populations of both heterotic groups in 16 – 18 different environments, covering a wide range of climatic and soil conditions. In six out of these 16-18 environments we conducted managed drought-stress field trials and evaluated each population. A high environmental variation was confirmed by a high variation in GY. A high proportion of G x E interaction variance at the total variance also confirmed the environmental differences. For all three populations the interaction variance (G x E) was two times larger than the genotypic variance calculated over all environments. With a low G x E interaction the optimum number of environments can be reduced and more candidates can be evaluated to increase the selection gain. If the G x E interaction variance is high, more environments should be included while fewer candidates can be tested. The impact of the G x E variance leads to the choice of the appropriate breeding strategy to develop varieties for a given range of target environments (Tomerius, 2001). Tomerius (2001) mentioned two options for breeding strategies: (1) to develop new varieties for specific environments in smaller breeding programs, or (2) to run only one breeding program to develop varieties adapted to the whole range of environments. The G x E interaction variance will increase with increasing environmental heterogeneity of the target environment. It is advantageous to employ one breeding program across two zones as long as the increase of the G x E is not too strong (assuming a 1.5 fold increase of the interaction variance). The number of candidates can be twice as large and the number of locations can also be higher in comparison to site specific breeding programs, assuming the same budget.

We focused on important agronomic traits, but GY was the most sensitive trait compared to TGW, PH and HT. In 15 out of 18 managed drought-stress

environments we observed significantly lower GY (2–40%, see section III), but only nine environments showed a significant G x I interaction. Our observed low G x I interaction (see section III) also shows that rye is well adapted to marginal environments, which has already been observed in other publications (Hoffmann, 2008; Hübner et al., 2013). For breeders significant G x I interaction variance would be interesting for developing more drought tolerant genotypes. The G x I variance represent only a small part of the total variance. And even though the G x E x I interaction variance also includes the G x I interaction, this part is not utilized by the breeder. The significant G x E x I interaction variance indicated, that every environment suffered from different drought stress.

We observed highly stable genotypes for GY over a wide range of test environments. Almost all genotypes were highly stable (653 out of 658 genotypes) over 16 – 18 environments (section III). All three populations were already adapted similarly to both low and high yielding environments with almost all progenies. Breeding on less fertile and sandy soils led to stress tolerant hybrids. However, the range of genotypes above and below average in yield stability enables breeders to select for high yield stability. An important objective is the difference between morphological and physiological characters. Different studies in wheat and barley under drought stress pointed out that several morphological and physiological characters differ among high yielding varieties under stress and under optimum conditions (Ceccarelli et al., 1991; Ceccarelli and Grando, 1996).

Improvement of yield stability could be achieved by selecting for constitutive characters with low G x E interaction. Traits such as root number were already described in barley (Ceccarelli and Grando, 1991). In maize the use of optimal and managed drought stress environments is recommended in order to select for the broadest adaptation possible (Chapman et al., 1997). Chapman et al. (1997) recommend selection of broad adaptation (higher mean yield) and thereby increasing the specific adaptation to drought environments.

In general, drought stress is not as important as there is less G x I interaction and a high correlation of close to 1 of traits, such as PH, GY and TGW between

rained and irrigated conditions (see section III). This could suggest, that the elite rye material is already stress tolerant (Hoffmann, 2008; Hübner et al., 2013) or that the drought stress was not strong enough (Blum, 2005). This allows a combination of all environments into one analysis in order to improve conclusions on genetic variation for yield stability.

It is therefore, not necessary to develop special breeding programs for European rye production in dry environments, as long as drought does not occur regularly and yield reduction stays below 50 % (Blum, 2005). But selection and testing in different environments with diverse fertility and precipitation and managed-drought stress conditions should be conducted to achieve promising and stable rye varieties. They should also be capable of buffering high climate fluctuations that might occur in future climates.

Additional studies already exist for other crops to detect QTLs under drought conditions and there are promising possibilities to improve drought tolerance with marker information. A QTL on chromosome 4AL for wheat was found to have a significant influence on performance under reduced moisture. The QTL, which is associated with the microsatellite locus Xwmc89 had a significant influence on GY, grain filling rate, spike density, grains m⁻², biomass production, biomass production rate and drought susceptibility index (Kirigwi et al., 2007). One study detected 42 QTL for GY and growth traits on genome A and B (Maccaferri et al., 2008) and 16 QTL for GY and growth traits on genome A, B and D (Mathews 2008).

For barley, favorable QTL alleles from wild barley accession germplasm (HOR 11508) were identified by an advanced backcross QTL analysis (Talamè et al., 2004). Additionally a high number of QTL for GY, growth traits and other agronomic traits were detected in barley germplasm (Teulat et al., 2001; Baum et al., 2003; von Korff et al., 2008). QTL for GY were found in rice on chromosome 2 and 3 (Venuprasad et al., 2009) and chromosome 12 (Bernier et al., 2007, 2009). Several studies detected QTL in maize. 81 QTL were found for yield components and secondary traits (Messmer et al., 2009), 20 QTL for GY and yield components (Xiao 2005) and further 56 QTL for root characteristics, drought tolerance index

and GY (Tuberosa et al., 2002a). In addition, different examples already exist for MAS for drought tolerance. In rice, MAS back-crossing breeding program was conducted to improve root characteristics in rice. Four QTL for improving root length and thickness were used to improve drought tolerance (Steele et al., 2006, 2007). MAS backcrossing was also used in pearl millet where QTL had a significantly positive influence on grain yield under terminal stress (Serraj et al., 2005). In cotton near isogenic lines (NILs) were used to evaluate the development of drought tolerance by MAS. Using NILs may lead to better drought tolerance but must be combined with high grain yield (Levi et al., 2009). Using MAS to improve drought tolerance in the common bean led to 11 % higher yield performance under stress and 8 % under non stress conditions while conventional selection failed. (Schneider et al., 1997a; b). For maize, a further successful MAS back-crossing was described to improve drought tolerance using QTL (Ribaut et al., 1996; Ribaut and Ragot, 2006).

We found different QTL for the traits HT, PH, GY and TGW under both water regimes for Pop-C (Table 10). Only three QTL for PH and one QTL for TGW were found under both water regimes.

Table 4. Number (No.) of detected quantitative trait loci (QTL) for heading time (HT), plant height (PH), grain yield (GY) and thousand-grain weight (TGW) in each variant, and number of common QTL (\cap) for irrigated (I) and rainfed (R) regimes in Pop-C across six environments.

Trait	QTL I		QTL R		\cap
	No.	Total R ²	No.	Total R ²	No.
HT	3	35.65	-	-	-
PH	6	47.26	7	57.67	3
GY	1	15.38	1	10.42	-
TGW	2	16.41	6	72.94	1

Within the Petkus gene pool seven and four QTL were found for GY under irrigated and rainfed conditions, respectively. Two of these QTL were found under both regimes (Hübner, 2013). Dynamic genes have already been described for other crops like rice (Yan et al., 1998; Cao et al., 2001) and wheat (Zhang et al., 2013) under different environments. Therefore, much more work has to be

done to identify stable QTL for GY over a wide range of environments. Further, much more work has to be done to find also dynamic drought tolerant QTL within both heterotic groups, which would be an advantage to improve the yield level under drought conditions. In order to avoid drought stress, it could be promising to have QTL, which buffer dry spring and summer seasons by switching on drought-tolerant gene regions. Therefore we could concentrate and identify special QTL to buffer drought stress, as already described for other crops and mentioned above.

5.3. Conclusions for hybrid rye breeding

Modern hybrid rye varieties have great potential as an alternative biogas substrate. Either in regions where other crops are not economically feasible, agronomic diversity in crop rotation needs to be increased or for increasing the total biomass yield by harvesting two crops annually. In our studies we identified a high phenotypic correlation between PH and DMY. GY showed only a moderate correlation to DMY. Using PH as an indirect selection criterion will successfully increase DMY in modern rye breeding programs. The genotypic results underlined the phenotypic results by evidence of similar QTL for PH and DMY, due to the fact that both traits were highly correlated. Attention should be paid to highly dynamic QTL. We found different QTL for all PH (1-3) measurements, while only one QTL was found in common for PH 2 and PH 3. Introducing all dynamic QTL in new varieties could be difficult and time consuming. Therefore, one QTL (in PH 2 and PH 3) can be used to accelerate the breeding steps and modify PH. Above all, avoiding dwarf genes would be the simplest and fastest way to influence PH by using MAS (Alheit et al., 2014; Kalih et al., 2014). MAS is one opportunity, but it ignores the effect of small and intermediate QTL (Bernardo, 2008; Heffner et al., 2009). Therefore, genomic selection (GS) is suggested as an extension of MAS (Meuwissen et al., 2001). One study in rye pointed out, that GS is superior to MAS in selection of closely related candidates to the evaluated plant material (Wang et al., 2014a). Therefore, work has to be done to improve the accuracy of genotypic information and the application within

modern breeding programs. Whether or not these results lead to a paradigm shift in modern plant breeding programs, it is possible to increase DMY for modern hybrid rye varieties. Therefore, breeders have to concentrate on taller plants with a stronger focus on lodging resistance. In other crops already different phenotypic traits and also QTL were described to improve lodging resistance without decreasing PH (see chapter 5.1).

We showed that modern hybrid rye varieties are already stable over a wide range of different environments differing in climatic and soil conditions. Managed-drought stress trials showed high correlations between irrigated and rainfed conditions for all genotypes and agronomic traits. Significant yield reduction occurred in most environments. We observed yield reductions up to 40% between both water regimes, but only a few environments showed a significant $G \times I$ interaction. Drought tolerance is one the most important traits in modern breeding programs and should be included in their selection process. It is possible that our drought stress was not intense enough (Blum, 2005a) or rye is already drought tolerant (Hübner et al., 2013; see section III). Nevertheless, it will be essential to test modern hybrid rye varieties for drought tolerance as extreme weather events will have a stronger influence on our cultivated crops in the future (Ciais et al., 2005). Therefore we have to increase drought stress in field trials and discover when drought stress has the highest influence on grain and biomass yield. Currently, drought stress does not occur regularly or for long periods of time, but concentrating on high yielding and highly stable genotypes under these conditions will be important for future varieties. Generally, genotypes showed no difference between both water regimes, but it would be useful to include managed-drought stress trials in modern breeding programs to test advanced candidates under both regimes to confirm their above average yield. With modern breeding material, selection for highly stable genotypes for a wide range of environments is possible and should be carried out to achieve favourable high yielding varieties for GY and DMY.

It is important to specify and combine phenotypic and genotypic data for a better understanding of mechanisms that are responsible for high yields and stability in

hybrid rye. We have to improve and specify two factors: on one hand the collection of phenotypic data and, on the other hand the effective use of genetic markers and their genotypic information. First, phenotypic data collection should become more precise. Collection of phenotypic data has reached a new level with the introduction of phenotyping platforms where a multiplicity of data can be collected at once. Phenotyping platforms may be a promising tool for increasing the accuracy of phenotypic data. A new tractor-pulled multi-sensor phenotyping platform for small grain cereals allows the observation of various agronomic traits, such as plant moisture content, lodging, tiller density or biomass yield (Busemeyer et al., 2013) and provides a great opportunity for applying non-destructive phenotyping for crop improvement and plant genetic studies.

Secondly, the quantity and quality of genotypic data in rye has to be improved. Marker technologies have become faster and cheaper and gaining in importance as well as applicability in all plant breeding programs. For most of the major crops more sophisticated and complex methods (e.g. genomic selection, novel transgenics), are being developed and increasingly introduced into commercial breeding programs. Although large numbers of genetic markers are now available for most of the main cereal crops (e.g. a rice already 44k SNP chip (Zhao et al., 2011), a maize 600k SNP (Unterseer et al., 2014) and a wheat 90k SNP chip (Wang et al., 2014b) already exist), only a 5k SNP chip for rye is currently available (Haseneyer et al., 2011) and a 20k SNP will soon be available (Bauer, pers. commun.). For rice and maize a 700k SNP chip will be introduced soon. Another opportunity would be genotyping by sequencing (GBS), which is a cost-efficient, technically simple, and highly multiplex-able method feasible for high diversity and large genome species. The method is used to reduce genome complexity with restriction enzymes. Fragments of specific size are sequenced and representing a part of the whole genome. Due to the reduction of the genome more individuals can be sequenced together. GBS will facilitate the use of genomic-assisted breeding on novel germplasm without developing prior molecular tools and determining population structure even in the absence of a reference genome (Elshire et al., 2011; Poland et al., 2012).

Our results for different QTL under irrigated and rainfed conditions give a hint that different genes are expressed under different environments. Up to now we are far behind in understanding the mechanisms, which are exploited under different water regimes. Therefore, we have to concentrate on traits in detail and plant physiological aspects in order to specify single and complex plant mechanisms under different drought conditions. Out of it we can define key traits, which play an important role in drought tolerance mechanisms (Cooper et al., 2014). In consideration of these aspects the genotypic information by markers should be enlarged in order to perform accurate genetic evaluation of plant material for selection in all stages of the breeding program (Cooper et al., 2014). These points will lead to high and stable yielding varieties and will contribute to enhance food production in our agricultural systems.

6. Summary

Rye is an important crop in Northern and Eastern Europe and mainly used for food and feed and became most recently important for biogas production. Hybrid rye varieties dominate the cultivated area, which is mainly on light and sandy soils, because rye has a relatively high tolerance to biotic and abiotic stress factors. Climate change will also affect Central Europe, causing higher temperatures and less precipitation in spring and summer. Rye will be influenced more by these effects than other cereals because it is mainly grown on marginal environments.

Rye has a high potential for being used as a biogas substrate, but detailed information on improving this trait in hybrid rye is missing. Until now, no study that analyzed phenotypic and genotypic agronomic traits for using rye for biogas production exists. Further, there is only one study, which dealt with the influence of periodic drought stress in rye cultivated areas. Beside this, we analyzed yield stability over a wide range of environments in consideration of drought stress in Central Europe.

We analyzed an interpool hybrid population (Pop-D) in 2011 and 2012 at seven environments in Germany for the biomass yield and grain yield (Publication I). This study showed low correlations between grain yield and dry matter yield ($r = 0.33$). Higher correlations were obtained with two plant height measurements (at heading time, $r = 0.64$; before harvest, $r = 0.52$) and dry matter yield. The indirect selection via plant height was superior in contrast to the direct selection of dry matter yield by factor 1.24. Genotypic results confirmed phenotypic results as no overlapping QTL for grain yield and dry matter yield were detected (Publication II). However, we identified common gene regions for plant height and dry matter yield due to the high correlation between both. Plant height is a promising trait for indirectly selecting high biomass yielding varieties. The paradigm shift from shorter plants with high grain yield to taller hybrids as a resource for biogas substrate needs additional breeding efforts for lodging resistance.

In Publication III we analyzed two intrapool populations (Pop-A and -B) and one interpool population (Pop-C) at 16 – 18 environments (location x year

combinations) under irrigated and rainfed conditions in Germany and Poland. Yield stability was high over a wide range of environments, even when drought stress environments were included. This illustrates the adaption of rye to marginal and drought stress environments. The analyzed populations showed no differences within yield stability, but yield differences between inter- (Pop-C) and intra-pool (Pop-A and -B) crosses were visible. Selection for yield stability is possible due to the genetic variance for this trait within all three populations. Therefore, it is important to select genotypes with low genotype x environment interaction. All three populations showed high yield stability on a high yield level and were already well adapted to extreme weather events caused by climate change. It is recommended to use highly diverse environments with irrigated and rainfed conditions to select on yield stability and high yielding varieties under optimum and drought conditions.

7. Zusammenfassung

Roggen ist eine Kulturart des nord- und osteuropäischen Raumes und neben seiner Hauptnutzung als Brot- und Futtergetreide wird Roggen auch zunehmend zur Biogasproduktion verwendet. Hybridsorten dominieren den Anbau, der meist auf leichten und sandigen Böden erfolgt, da Roggen biotischen und abiotischen Stress besser als andere Kulturarten toleriert. Durch den weltweiten Klimawandel ist auch Zentraleuropa von zunehmenden Wetterextrema betroffen, die höhere Temperaturen und weniger Niederschlag im Frühjahr und Sommer hervorrufen, Roggen wird von diesem Einfluss stärker als andere Kulturarten betroffen sein, da der Anbau meist auf marginalen Böden erfolgt.

Roggen weist ein hohes Potential zur bioenergetischen Nutzung auf, allerdings existiert bisher keine Studie, die phänotypische und genotypische Parameter zur Nutzung von Roggen zur Biogasproduktion näher untersucht hat. Ebenso gibt es bisher nur eine Studie, die sich genauer mit dem periodischen Einfluss von Trockenstress auf den Roggenanbau befasst hat. Daher untersuchten wir die Ertragsstabilität über eine Vielzahl an Umwelten in Zentraleuropa unter der Berücksichtigung von reduziertem Wasserangebot.

Wir untersuchten eine Interpool-Population (Pop-D) in 2011 und 2012 in sieben Umwelten in Deutschland auf ihre Biomasse- und Kornertragsleistung (Publikation I). Die Korrelation zwischen Kornertrag und Trockenmasseertrag mit $r = 0.33$ war gering. Höhere Korrelationen wurden zwischen zwei Wuchshöhemessungen zum Zeitpunkt des Ährenschiebens ($r = 0.64$) und der Abreife ($r = 0.52$) und dem Trockenmasseertrag bestimmt. Die indirekte Selektion auf Wuchshöhe war der direkten Selektion auf Trockenmasseertrag relativ um den Faktor 1,24 überlegen.

Die genetische Architektur dieser Merkmale untermauerte die phänotypisch dargestellten Ergebnisse (Publikation II). Wir identifizierten Quantitative-Trait Loci (QTL), die für die Ausprägung der Wuchshöhe und der Trockenmasse verantwortlich sind, wobei es keine Übereinstimmungen zwischen Trockenmasse und Kornertrag gab. Das Merkmal Wuchshöhe eignet sich besonders für eine indirekte Selektion auf biomassestarke Typen. Der damit verbundene Paradigmenwechsel von kürzeren und standfesten Hohertragssorten für den

Kornertrag hin zu wuchsstarken Hybriden für die Biogasproduktion muss aber mit einem verstärkten Focus auf Standfestigkeit einhergehen.

In Publikation III wurden zwei Intrapool-Populationen (Pop-A und -B) und eine Interpool-Kreuzung (Pop-C) an insgesamt 16 – 18 Umwelten (Ort x Jahr Kombinationen) in Deutschland und Polen unter bewässerten und unbewässerten (regenabhängigen) Bedingungen analysiert.

Die Ertragsstabilität der Hybriden über die Vielzahl an Umwelten war hoch, sogar wenn Trockenstressumwelten in die Analyse einfließen. Dies verdeutlichte die Anpassung von Roggen an marginale und Trockenstressumwelten. Zwischen den untersuchten Populationen gab es dabei keine Unterschiede in der Ertragsstabilität, allerdings zeigte sich der Ertragsunterschied zwischen der Interpool-Kreuzungen (Pop-C) und den Intrapool-Kreuzungen (Pop-A und Pop-B). Züchterisch kann in dem untersuchten Elitematerial allerdings noch auf Ertragsstabilität selektiert werden, da beim Kornertrag innerhalb der Populationen eine genetische Variation vorhanden ist. Für die weitere Züchtung ist es daher wichtig Genotypen mit einer geringen Genotyp x Umwelt Interaktion zu selektieren. Insgesamt zeigten die drei untersuchten Populationen bereits eine hohe Ertragsstabilität auf einem hohen Ertragsniveau und sind an Wetterextreme, die durch den Klimawandel häufiger auftreten angepasst. Es wird vorgeschlagen in Zukunft unterschiedliche Umwelten mit bewässerten und unbewässerten Bedingungen zu kombinieren, um auf Ertragsstabilität und Hohertragstypen unter optimalen und Trockenstressbedingungen zu selektieren.

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Danke!

10. Curriculum vitae

PERSONAL

Born on 17.12.1982 in Salzgitter Lebenstedt

EDUCATION AND CAREER

- Consultant 01.2015 - today
National and International Variety and Seed Affairs
Coordination Centre for the Ministry of Food and Agriculture
Federal Plant Variety Office – Hannover
- PhD 02.2011 - 06.2015
Topic: “Quantitative-trait loci (QTL) mapping of important
agronomical traits of the grain and biomass production in winter rye”
State Plant Breeding Institute – University of Hohenheim
- Teacher in the area of crop production 01.2012 - 07.2013
State school for horticulture and agriculture, Stuttgart Hohenheim
- Diploma in Agricultural Biology 10.2005 - 02.2011
Diploma thesis: “Assessment of different methods of farmer-participatory selection in
diversified pearl millet populations at three pilot sites in Niger”
University of Hohenheim
- Employment as a banker 01.2005 - 09.2005
Special department for the implementation of the merger
Hypovereinsbank AG – Vereins- und WestBank AG
HVB-Profil AG, Hamburg
- Training as a banker 08.2002 - 01.2005
Vereins- und Westbank AG, Braunschweig, Hamburg, Hannover, Hildesheim
- School education (Degree: Abitur) 08.1995 - 07.2002
Gymnasium Groß Ilsede

PRACTICAL ACTIVITIES

- Department of pearl millet breeding 08.2009 - 11.2009
International Crop Research Institute of the Semiarid Tropics (ICRISAT) Niamey - Niger
- Student assistant in the Laboratory of Plant Breeding Institute 04.2009 - 07.2009
Universität Hohenheim
- Department of blunt breeding of rapeseed 07.2008 - 09.2008
Limagrain Germany GmbH, Breeding station Rosenthal – Lower Saxony
- Volunteer training program 08.2007
Southern African Wildlife College, Krüger Nationalpark, Southafrica
- Employee at winery 08.2006 - 10.2006
Weinbau Maier, Schwaikheim – Baden Württemberg

UNIVERSITY POLITICAL COMMITMENT

Member of the Research Committee	06.2012 - 09.2014
Member of the Senate	10.2007 - 09.2009
Chairman of the General Student Committee	06.2007 - 09.2009
Member of the General Student Committee	10.2006 - 09.2009
Member of the Commission Tuition	10.2006 - 09.2008
Member of Student Union Agricultural Biology	04.2006 - 02.2011

IT AND LANGUAGES

MS Office, statistical packages (PLABSTAT, Genstat, R) Joinmap

German - mother tongue, English - fluent, French - basics

SCHOLARSHIPS / AWARDS

Fellow of Ulm Panis Foundation

Support of diploma thesis

Award for outstanding student commitment

University of Hohenheim

11. Erklärung

Eidesstattliche Versicherung gemäß § 8 Absatz 2 der Promotionsordnung der Universität Hohenheim zum Dr.sc.agr.

Bei der eingereichten Dissertation zum Thema

“Quantitative-trait loci (QTL) mapping of important agronomical traits of the grain and biomass production in winter rye (*Secale cereale* L.)”

handelt es sich um meine eigenständig erbrachte Leistung.

Ich habe nur die angegebenen Quellen und Hilfsmittel benutzt und mich keiner unzulässigen Hilfe Dritter bedient. Insbesondere habe ich wörtlich oder sinngemäß aus anderen Werken übernommene Inhalte als solche kenntlich gemacht.

Ich habe nicht die Hilfe einer kommerziellen Promotionsvermittlung oder -beratung in Anspruch genommen.

Die Bedeutung der eidesstattlichen Versicherung und der strafrechtlichen Folgen einer unrichtigen oder unvollständigen eidesstattlichen Versicherung sind mir bekannt.

Die Richtigkeit der vorstehenden Erklärung bestätige ich. Ich versichere an Eides statt, dass ich nach bestem Wissen die reine Wahrheit erklärt und nichts verschwiegen habe.

Stefan Haffke