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HOHENHEIM

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Prospects of genomic selection for disease resistances in winter wheat (*Triticum aestivum* L.)

Dissertation

Submitted in fulfillment of the requirements for the degree
„Doktor der Agrarwissenschaften“
(Dr. sc. agr. /Ph. D. in Agricultural Sciences)
to the Faculty of Agricultural Sciences

Presented by
Master of Science
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from Berlin

Stuttgart – Hohenheim

2019

This thesis was accepted as a doctoral dissertation in fulfillment of the requirements for the degree “Doktor der Agrarwissenschaften” (Dr. sc. Agr. / Ph. D. in Agricultural Sciences) by the Faculty of Agricultural Sciences at the University of Hohenheim, on May 2019.

Day of oral examination: 11.12.2019

Examination Committee:

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This PhD thesis was funded by the German Federal Ministry of Education and Research (BMBF, Grant no. 031B0011A+E) in the framework of Bioeconomy International (FusResist).



Federal Ministry
of Education
and Research

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^{II} Miedaner T, Herter CP, Ebmeyer E, Kollers S, Korzun V (2019) Use of non-adapted quantitative trait loci for increasing Fusarium head blight resistance for breeding semi-dwarf wheat. *Plant Breeding* 138:140-147. doi: 10.1111/pbr.12683

^{III} Herter CP, Ebmeyer E, Kollers S, Korzun V, Würschum T, Miedaner T (2018) Accuracy of within- and among-family genomic prediction for Fusarium head blight and *Septoria tritici* blotch in winter wheat. *Theoretical and Applied Genetics* 132:1121-1135. doi: 10.1007/s00122-018-3076-8

^{IV} Herter CP, Ebmeyer E, Kollers S, Korzun V, Miedaner T (2019) An experimental approach for estimating the genomic selection advantage for Fusarium head blight and *Septoria tritici* blotch in winter wheat. submitted to *Theoretical and Applied Genetics* 132:2425-2437, doi: 10.1007/s00122-019-03364-7

ABBREVIATIONS

BLUES	best linear unbiased estimators
DON	deoxnivalenol
DS	data set
EG-BLUP	extended genomic-estimated linear unbiased prediction
FHB	Fusarium head blight
GA	gibberellic acid
GE	genotype \times environment interaction
GEBV	genomic estimated breeding value
GS	genomic selection
GWAS	genome-wide association study
LD	linkage disequilibrium
MAS	marker-assisted selection
<i>Ppd</i>	photoperiod response gene
PS	phenotypic selection
QTL	quantitative trait locus
<i>Rht</i>	reducing height gene
RKHSR	kernel Hilbert space regression
RR-BLUP	ridge regression-best linear unbiased prediction
STB	Septoria tritici blotch
wRR-BLUP	weighted ridge regression-best linear unbiased prediction
ZON	zearalenone

1 GENERAL INTRODUCTION

Wheat (*Triticum aestivum*) is the most cultivated crop worldwide with a global output of 749 million tonnes in 2016 (FAOSTAT 2018). Growing areas range from the southern regions of South America and Australia to the northern latitudes of Canada and China (Bushuk 1997). Wheat tolerates a wide range of climatic conditions, soil fertility, and elevations. As a valuable source of protein, vitamins and minerals it is the most important food grain and provides over 20 % of the calories in human nutrition. It can be stored over long periods and easily transported. Wheat originated from hybridization between cultivated tetraploid emmer wheat (AABB, *Triticum dicoccoides*) and diploid goat grass (DD, *Aegilops tauschii*) approximately 10,000 years ago (Salamini et al. 2002; Petersen et al. 2006). The domestication of wheat took place in the Middle Eastern region known as the Fertile Crescent (Feuillet et al. 2008), where the early plant breeders were farmers who genetically improved wild cereals predominantly by phenotypic mass selection for desired traits like non-brittle rachis, non-shattering of seeds, free threshing, and increased grain size (Murphy 2007). The cultivation value of wheat increased by the selection of these traits and its allopolyploid nature contributed furthermore a broad adaption to various growing areas. However, it took several thousand years until the cultivation of wheat spread into the common growing areas known today (Harlan 1981). Improved crop management practices in combination with modern plant breeding methods and technologies resulted in an average grain yield of 3 t ha⁻¹ (FAOSTAT 2018).

FUSARIUM HEAD BLIGHT – THE MOST DEVASTATING WHEAT DISEASE WORLDWIDE

Fusarium head blight (FHB) is an economically important disease on small grain cereal crops in humid and semi-humid areas worldwide (Schroeder and Christensen 1963; Steffenson 2003). Although many Fusarium species can cause FHB, *Fusarium graminearum* is the most common pathogen in many countries (Schroeder and Christensen 1963; Sutton 1982; Wang and Miller 1988; Bai and Shaner 1994). FHB causes quality reduction by contamination of harvested grain with potent mycotoxins, especially high levels of deoxynivalenol (DON) and zearalenone (ZON), and up to 40 % yield loss (Parry et al. 1995; McMullen et al. 1997; Bai et al. 2001). The maximum acceptable DON and ZON values for human consumption in raw wheat grain are limited to 1,250 µg kg⁻¹ and to 100 µg kg⁻¹, respectively, in the European Union ((EG)

Nr. 1126/2007) and obligate breeding companies to achieve at least a moderate resistance. As FHB can only partially be controlled by appropriate use of fertilizers, suitable crop rotation, soil tillage, weed control, and fungicide application with the dose and timing of spraying being a crucial factor (McMullen et al. 1997; Pirgozliev et al. 2003; Yuen and Schoneweis 2007; Willyerd et al. 2012). Additionally, the cost of treatment and the lack of highly effective

registered fungicides are limiting the usage of chemical protection against FHB. The best application may reduce direct yield loss up to 50 % in terms of damaged kernels, but mycotoxin contamination still forms a constant risk to the food chain (Martin and Johnston 1982; Magan et al. 2002; Ramirez et al. 2004; Paul et al. 2008). Consequently, the development of resistant varieties is the most effective approach for managing FHB. Two major types of resistance have been classified: resistance to initial infection (Type I) and resistance to spreading within a spike (Type II, Schroeder and Christensen 1963). Mesterházy (1995) further described additional types of resistance.



Fig. 1 Spike infected with FHB

SEPTORIA TRITICI BLOTCH – A LEAF DISEASE ADVANCING FAST

Septoria tritici blotch (STB), caused by *Zymoseptoria tritici*, is one of the most destructive foliar diseases of wheat (Eyal 1987; Eyal et al. 1987). Severe epidemics reduce yield and quality, and losses of up to 60 % have been reported for susceptible cultivars (Shipton et al. 1971; King et al. 1983; Eyal et al. 1985). STB was considered to be confined to Mediterranean-type climates with wet winters and temperate temperatures and in the ‘Great Plains’ of North America (Leath et al. 1993). In the recent years, STB is also spreading in the humid regions of the Maritimes Zones of Great Britain and Central Europe (Fones and Gurr 2015). This can be attributed to the widespread growing of early-maturing, short straw, susceptible cultivars, early sowing, increased nitrogen fertilizer, direct sowing, high summer rainfall and differential response to certain fungicides (Eyal 1999; Cools and Fraaje 2008; Torriani et al. 2009). Furthermore, long-term effectiveness of major resistance genes is lacking (Ahmed et al. 1995; Jackson et al. 2000; McDonald and Linde 2002). However, even in STB-prone regions, severe epidemics arise sporadic making control strategies more challenging (Eyal 1999). Resistance breeding of



cultivars, which provide durable resistance to STB is the most preferable method for controlling the disease.

Fig. 2 Leaves infected with STB

REDUCING PLANT HEIGHT GENES

In wheat, an agronomic trait of high importance is plant height. Plant height has a considerable influence on yield and quality traits as it determines the susceptibility to lodging. Therefore, over several decades, the development of short straw wheat has been an important breeding goal (Griffiths et al. 2012). During the ‘Green Revolution’ reducing plant height (*Rht*) or dwarfing genes had led to remarkable increases in grain yield and are intensively used in breeding programs worldwide (Hedden 2003). To date, more than twenty *Rht* genes have been identified in wheat, but most of them needs to be validated as their effects on agronomic traits have not been extensively examined (McIntosh et al. 2017). The most commonly utilized semi-dwarfing alleles are *Rht-B1b* and *Rht-D1b*, which are located on the chromosomes 4B and 4D at homoeologous loci, respectively, and the allele *Rht8c* on chromosome 2D. These alleles, derived from the non-adapted cultivars ‘Norin 10’ and ‘Akakomugi’, respectively, act as repressors of growth and are present in approximately 50 % of the worldwide wheat cultivars (Gale and Youssefian 1985; Archard et al. 2006; Wilhelm et al. 2013). Wheat varieties with dwarfing alleles are highly resistant to lodging as they are defined by stiff and short straw. This enables a rise of the harvest index as agronomic methods, such as applications of pesticides, irrigation, and nitrogen, can be intensified. Additionally, the *Rht-B1b* and *Rht-D1b* dwarfing alleles are correlated with the main yield components as they increase grain size, grain number per ear, grain fertility, tiller number and, hence, lead to increasing wheat yield (Gale and Youssefian 1985; Flintham et al. 1997; Li et al. 2006). Cultivars carrying the semi-dwarfing

alleles of *Rht-B1* and *Rht-D1* are characterized by a reduction of sensitivity to gibberellic acid (GA) and, consequently, reduced plant height (Peng et al. 1999). In contrast, the widely used locus *Rht8* is part of the GA sensitive dwarfing genes that restrain plant growth (Korzun et al. 1998; Worland et al. 1998).

ASSOCIATION OF FHB AND STB WITH AGRONOMIC TRAITS

A negative relationship between plant height and FHB has been observed in many studies (Zhu et al. 1999; Draeger et al. 2007; Klahr et al. 2007; Voss et al. 2008; Buerstmayr et al. 2009; Srinivasachary et al. 2009; Yan et al. 2011; Lu et al. 2013). This reduced resistance is considered to be directly affected by (semi-) dwarfing alleles and not just indirectly by plant height *per se* (Draeger et al. 2007; Gosman et al. 2008; Voss et al. 2008; Srinivasachary et al. 2009). Srinivasachary et al. (2009) reported, that the increase of FHB susceptibility was higher in presence of the semi-dwarfing allele *Rht-D1b* in comparison to the *Rht-B1b* allele. Miedaner and Voss (2008) announced reduced FHB resistance in varying degrees depending on the genetic background for the *Rht* alleles *Rht-B1b* and *Rht-D1b*. A negative association was further reported between FHB and heading date, inflorescence and anther extrusion (Zhu et al. 1999; Klahr et al. 2007; Skinnes et al. 2008; Buerstmayr et al. 2009; Lu et al. 2013).

Several authors have shown a relationship between STB and both, plant height and heading date (Shaner et al. 1975; Tavella 1978; Rosielle and Brown 1979; Rosielle and Boyd 1985; Baltazar et al. 1990; Camacho-Casas et al. 1995). Shaner et al. (1975) observed that flag leaves often emerge on early-maturing cultivars when the weather conditions are favorable for the disease in early spring (cool temperatures and rain). Other authors assumed the association between heading date and STB due to genetic linkage (Rosielle and Boyd 1985; Baltazar et al 1990). For this reason, the replacement of traditional tall cultivars by high-yielding, semi-dwarf varieties has increased severity levels in many parts of the world (Eyal 1987). However, Baltazar et al. (1990) observed differences in levels of resistance to STB depending on the present dwarfing gene. Simón et al. (2004) analyzed the influence of *Rht* genes on reaction to STB and detected no association with *Rht-D1b* in two sets of near isogenic lines. The authors announced the association of reduced plant height and enhanced STB severity primarily to lower distances between leaf insertions, making inoculum transfer easier, but only in very short wheat genotypes carrying the dwarfing alleles of the loci *Rht3* and *Rht12*, respectively. Arama et al. (1999), however, did not find genetic associations between plant height and STB severity

or heading date. Indeed, Van Beuningen and Kohli (1990) accounted these associations to epidemiological factors.

Lower disease coverage on the upper leaves and ears, respectively, contributed by tall plant stature due to disease escape and late maturity, can be announced as one resistance factor (Mesterházy 1995; Eyal 1999). However, the requirements for modern wheat cultivars are early maturity and short straw. Dwarfing loci causing short and stiff straw in wheat without simultaneously reducing FHB and STB resistance are therefore urgently required.

BREEDING FOR FHB AND STB RESISTANCES

The development of resistant cultivars is considered to be the most promising method for the management of both diseases, FHB and STB. Nevertheless, phenotypic selection for both diseases by direct symptom evaluation is time- and labor-intensive (Miedaner et al. 2012). Furthermore, conventional breeding for STB resistance is complicated by the long latent period of the disease, a great variability in the pathogen population, and a certain degree of specificity (Perelló et al. 1991; Adhikari et al. 2004). Marker-assisted selection (MAS) has been assumed to be an appropriate alternative to phenotypic selection and this approach enhanced disease resistances when few quantitative trait loci (QTL) of at least intermediate effect were present (Del Blanco et al. 2003; Yang et al. 2003; Zhou et al. 2003; Adhikari et al. 2004; Chartrain et al. 2005; Miedaner et al. 2006; Anderson et al. 2007; Goodwin 2007; McCartney et al. 2007; Wilde et al. 2007; Von der Ohe et al. 2010; Salameh et al. 2011; Agostinelli et al. 2012; Balut et al. 2013). Indeed, MAS was successfully implemented for FHB resistance conferred by the major QTL *Fhb1* in Northern American wheat breeding programs where this fungal disease has a very high economic impact (Steiner et al. 2017). *Fhb1* as well as the major QTL *Fhb5* (formerly called *Qfhs.ifa-5A*) are both derived from the cross ‘Sumai#3’×‘Thornbird-S’ (Buerstmayr et al. 2002, 2003). *Fhb1* belongs to Type II resistance while *Fhb5* was described as Type I resistance. Both loci are located on chromosome 3BS and 5B, respectively (Buerstmayr et al. 2002, 2003). However, as strategy of targeting mostly single QTL or genes, the advantages of MAS are restricted, because (1) large-effect QTL are absent in European breeding material (Holzapfel et al. 2008; Buerstmayr et al. 2009; Löffler et al. 2009; Miedaner et al. 2011; Miedaner and Korzun 2012; Mirdita et al. 2015a), (2) the risk of fixing large genomic regions is given, especially when linkage disequilibrium (LD) is large as in wheat, and (3) a high selection pressure is exerted on the pathogen populations. Indeed, when STB resistance breeding has been concentrated on monogenic, isolate-specific resistances STB

resistance was readily overcome (Ahmed et al. 1995; Jackson et al. 2000; McDonald and Linde 2002). Furthermore, experience with MAS in wheat indicates, that the effects of FHB QTL are often dependent on the genetic background and, thus, the potential of MAS to increase disease resistance occurs to be limited (Jiang et al. 2017). An additional obstacle hindering the broad application of MAS in the past were high genotyping costs. In recent years these costs have strongly declined making it possible to genotype large numbers of individuals with marker densities covering the entire genome (Elshire et al. 2011; Poland et al. 2012; Heslot et al. 2013). Genomic selection (GS), taking into account all QTL underlying a trait of interest, has been promoted as an alternative concept for selection of quantitative traits (Meuwissen et al. 2001; Goddard and Hayes 2007). Firstly, a large training population of intensively phenotyped individuals must be genotyped with a large number of genome-wide distributed markers. This training population is subsequently used to train a prediction model employing the marker genotypes as explanatory variables (Heffner et al. 2009; Jannink et al. 2010). This prediction model can finally be used to estimate genomic breeding values (GEBVs) for all genotyped selection candidates of whom no phenotypic information about traits of interest (e. g. grain yield or resistances to diseases) is available yet by summing up across all their estimated marker effects (Jannink et al. 2010). In this way, the GEBVs can support breeders in their selection decisions, by providing them more information about their breeding material in earlier phases of variety development. Indeed, GS has been shown to be promising for traits with complex inheritance which are controlled by many loci of small effect (Daetwyler et al. 2010; Jannink et al. 2010; Burgueño et al. 2012; González-Camacho et al. 2012). The ridge regression-best linear unbiased prediction (RR-BLUP) is a commonly used prediction model. This method shrinks all marker effects towards zero as it assumes that all markers share a common variance. Thus, the assumption of RR-BLUP is that many loci of small effect control a trait of investigation (Lorenz et al. 2011). However, when an appreciable proportion of the phenotypic variation is contributed by major QTL or genes, such as the QTL *Fhb1* or *Fhb5* for FHB resistance and the major genes *Stb1-Stb8*, *Stb10-Stb12* or *Stb15* for STB resistance (Goodwin 2007), RR-BLUP may underestimate the variance connected with these major genes or QTL. In such cases, the Bayesian GS models can capture the variance more appropriately by treating markers of different effect size heterogeneously (Habier et al. 2011; Resende et al. 2012). However, a remarkable disadvantage of Bayesian GS methods is that they are computational highly demanding. An alternative method that treats known functional markers as fixed effects, called weighted RR-BLUP (wRR-BLUP), was proposed by several authors (Bernardo 2014; Rutkoski et al. 2014; Arruda et al. 2016; Spindel et al. 2016; Michel et al. 2018).

GS could provide a durable and higher quantitative disease resistance to FHB by supporting the accumulation of many alleles of small effect (Rutkoski et al. 2012; Arruda et al. 2015; Mirdita et al. 2015a and 2015b; Poland and Rutkoski 2016) and STB (Mirdita et al. 2015a; Juliana et al. 2017a). However, these promising results arise from cross-validation studies within diversity panels or single bi-parental populations and the true phenotypic performance can only be determined after selection in the next growing session. Commonly, 80 % of a given data set is sampled as training population and used to fit a GS model to predict the remaining 20 % of the data set forming the validation population of whom the available phenotypic data is masked. This method is usually repeated several hundred times with varying training and validation population combinations. Following, the prediction ability can be determined as the correlation between predicted and observed performance in the validation population, which might be divided by the square root of the heritability to yield prediction accuracy (Dekkers 2007). However, this procedure does not represent the circumstances in wheat breeding programs where many new bi-parental crosses of mostly small size are produced every year (Bernardo 2003). So far, this fact is often given little attention in research (Bassi et al. 2016). In a recent study, Jiang et al. (2017) predicted FHB resistance among independent samples and yielded prediction accuracies comparable high to cross-validation. They assumed this result to be a consequence of the considerable relationship between the validation and the training set utilized in their study. Other independent validation studies are required, especially for important quantitative resistances to FHB and STB.

OBJECTIVES

The aim of this thesis was to investigate the potential of genomic selection across different genetic backgrounds, considering the reduced height loci *Rht24*, *Rht-D1* and the FHB resistance QTL *Fhb1* and *Fhb5* and its success for improving disease resistances in winter wheat.

In particular, the objectives were to

- (i) Evaluate the effect of the *Rht24* locus on FHB and STB resistances, plant height, and heading date in comparison to *Rht-D1* in the bi-parental winter wheat population ‘Solitär × Bussard’.
- (ii) Compare the effects of the *Rht-D1*, *Fhb1* and *Fhb5* loci on FHB resistance in a large pool of winter wheat lines.
- (iii) Analyze the prediction accuracy achieved by cross-validation in two large winter wheat populations and by within- and among-family prediction comparing the two prediction models RR-BLUP and wRR-BLUP for FHB and STB resistances, plant height and heading date.
- (iv) Quantify the genomic selection advantage and determine the percentage of correctly selected top 10 % individuals for FHB and STB resistances.

2 PUBLICATION: DWARFING GENES AND FUSARIUM HEAD BLIGHT¹

RHT24 REDUCES HEIGHT IN THE WINTER WHEAT POPULATION ‘SOLITÄR × BUSSARD’ WITHOUT ADVERSE EFFECTS ON FUSARIUM HEAD BLIGHT INFECTION

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Theoretical and Applied Genetics (2018) 131:1263–1272, doi: 10.1007/s00122-018-3076-8

The original publication is available at

<https://doi.org/10.1007/s00122-018-3076-8>

Abstract

The introgression of the Green Revolution semi-dwarfing genes *Rht-B1* and *Rht-D1* led to spectacular increases in wheat grain yields. However, their application causes increased susceptibility to Fusarium head blight (FHB). Thus, *Rht* loci that hold the potential to reduce plant height in wheat without concomitantly decreasing FHB resistance are urgently required. The biparental population ‘Solitär × Bussard’ fixed for the *Rht-I* wild-type alleles, but segregating for the recently described gibberellic acid (GA)-sensitive *Rht24* gene, was analyzed to identify quantitative trait loci (QTL) for FHB severity, plant height, and heading date and to evaluate the effect of the *Rht24* locus on these traits. The most prominent QTL was *Rht24* on chromosome 6A explaining 51% of genotypic variation for plant height and exerting an additive effect of – 4.80 cm. For FHB severity three QTL were detected, whereas five and six QTL were found for plant height and heading date, respectively. No FHB resistance QTL was co-localized with QTL for plant height. In contrast to the *Rht-I* semi-dwarfing alleles, *Rht24b* did not significantly affect FHB severity. This underlines, that the choice of dwarfing alleles is a crucial factor for breeding FHB resistant wheat varieties.

3 PUBLICATION: EXOTIC FUSARIUM HEAD BLIGHT RESISTANCE QTL II

USE OF NON-ADAPTED QUANTITATIVE TRAIT LOCI FOR INCREASING FUSARIUM HEAD BLIGHT RESISTANCE FOR BREEDING SEMI-DWARF WHEAT

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Plant Breeding (2019) 138:140-147, doi: 10.1111/pbr.12683

The original publication is available at

<https://doi.org/10.1111/pbr.12683>

Abstract

Short and stiff straw is an important breeding goal in wheat breeding programs to develop high yielding varieties. In Northern Europe, this aim is achieved by using one of the dwarfing genes *Rht-B1* or *Rht-D1*. Both genes, however, result in a higher susceptibility to Fusarium head blight (FHB). We analysed the possibility to use the two non-adapted FHB resistance quantitative trait loci *Fhb1* and *Fhb5* (syn. *QFhs.ifa-5A*) to counterbalance the negative effect of the dwarfing allele *Rht-D1b* in a winter wheat population of 585 doubled-haploid (DH) lines segregating for the three loci. All genotypes were inoculated with *Fusarium culmorum* at four locations and analysed for FHB severity, plant height, and heading date. The DH population showed a significant ($p < 0.001$) genotypic variation for FHB severity ranging from 3.6% to 65.9% with a very high entry-mean heritability of 0.95. The dwarfing allele *Rht-D1b* reduced plant height by 24 cm, but nearly doubled the FHB susceptibility (24.74% vs. 12.74%). The resistance alleles of *Fhb1* and *Fhb5* reduced FHB susceptibility by 6.5 and 11.3 percentage points, respectively. Taken all three loci together, *Fhb5b* alone was already able to compensate the negative effect of *Rht-D1b* on FHB resistance. Marker-assisted introgression of *Fhb5b* might support semi-dwarf wheat breeding without decreasing FHB resistance.

4 PUBLICATION: GENOMIC SELECTION ^{III}

ACCURACY OF WITHIN- AND AMONG-FAMILY GENOMIC PREDICTION FOR FUSARIUM HEAD BLIGHT AND SEPTORIA TRITICI BLOTCH IN WINTER WHEAT

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Theoretical and Applied Genetics (2018) 132:1121–1135, doi: 10.1007/s00122-018-3264-6

The original publication is available at

<https://doi.org/10.1007/s00122-018-3264-6>

Abstract

Genomic selection (GS) is a valuable breeding tool that holds the potential to enhance selection gain in breeding programs by reducing the cycle length and/or increasing the selection intensity. In this study, two winter wheat populations (DS1 and DS2) comprising 438 and 585 lines derived from six and eight bi-parental families, respectively, were genotyped with genome-wide single nucleotide polymorphism markers and phenotyped for Fusarium head blight and Septoria tritici blotch severity, plant height and heading date. We used ridge regression-best linear unbiased prediction to investigate the potential of genomic selection under different selection constellations: prediction across each winter wheat population, within- and among-family prediction in each population, and prediction from DS1 to DS2 and vice versa. Additionally, we compared a full random model to a model incorporating quantitative trait loci (QTL) as fixed effects. The prediction accuracies obtained by cross-validation within populations were moderate to high for all traits. Accuracies for individual families were in general lower and varied with population size and genetic architecture of the trait. In the among-family prediction scenario, highest accuracies were achieved by predicting from one half-sib family to another, while accuracies were lowest between unrelated families. Our results further demonstrate that the prediction accuracy can be considerably increased by a fixed effect model approach when major QTL are present. In conclusion, the application of GS for Fusarium head blight and Septoria tritici blotch resistance breeding appears feasible, but the structure of the training population is a crucial factor for maintaining moderate prediction accuracies.

5 PUBLICATION: GENOMIC SELECTION ADVANTAGE ^{IV}

AN EXPERIMENTAL APPROACH FOR ESTIMATING THE GENOMIC SELECTION ADVANTAGE FOR FUSARIUM HEAD BLIGHT AND SEPTORIA TRITICI BLOTCH IN WINTER WHEAT

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Theoretical and Applied Genetics (2019) 132:2425-2437, doi: 10.1007/s00122-019-03364-7

The original publication is available at

<https://doi.org/10.1007/s00122-019-03364-7>

Abstract

Genomic selection (GS) holds the potential to accelerate the breeding cycle by facilitating the rapid selection of superior genotypes based on marker data solely. However, reported realized gain from genomic selection is limited to few experiments. In this study, a training population of 1120 winter wheat lines derived from 14 bi-parental families was genotyped with genome-wide single nucleotide polymorphism markers and phenotyped for Fusarium head blight (FHB) and Septoria tritici blotch (STB) severity, plant height and heading date. We used weighted ridge regression best linear unbiased prediction to calculate genomic estimated breeding values (GEBVs) of 2500 genotypes. Based on GEBVs, we selected the most resistant wheat lines as well as a random sample and tested them in a multi-location field trial. We computed moderate coefficients of correlation between observed and predicted trait values for FHB severity, plant height and heading date and achieved a genomic selection advantage of 10.62 percentage points for FHB resistance compared to the randomly chosen subpopulation. GS failed for the improvement of STB resistance with a genomic selection advantage of only 2.14 percentage points. Our results also indicate that the selection of new breeding parents based on GEBVs is not reliable. Taken together, the implementation of GS for FHB resistance, plant height and heading date seems to be promising. In contrast, for traits with very strong genotype \times environment variance, like STB resistance, the application of GS appears to be still challenging.

6 GENERAL DISCUSSION

The development of resistant cultivars through accumulation of resistance QTL is the most effective approach for managing FHB and STB leading to the enhancement of yield stability. However, resistance breeding faces several problems including labor- and time-intensive disease evaluations, negative associations of both diseases with plant height, and for STB a long latent period of the disease and a lacking durability of major resistance genes. Genomic selection (GS) has been examined in several studies for agronomic traits and appears to be a promising breeding tool in diverse crops.

The aim of this study was to improve the potential of resistance breeding for FHB and STB by employing GS as breeding tool, by analysis of the recently detected dwarfing gene *Rht24* as an alternative to the widely used locus *Rht-D1*, and by examination if the non-adapted FHB resistance QTL *Fhb1* and *Fhb5* might counteract the negative effect of *Rht-D1* on FHB resistance.

RHT24 AND ITS ASSOCIATION WITH PLANT HEIGHT AND FHB

The recently on chromosome 6A characterized gibberellic acid (GA) sensitive dwarfing gene *Rht24* appears in wheat varieties from USA, China, and Europe (McIntosh et al. 2017; Tian et al. 2017; Würschum et al. 2017a). Würschum et al. (2017a) reported, that the allele *Rht24b* is already extensively utilized in breeding programs worldwide as it was found in 67 % of the cultivars registered since 1990. The dwarfing allele, formerly called *QPH.caas-6A* (Li et al. 2015), is associated with increased number of spikes and kernel number per spike to a similar extent as *Rht-D1* and further with thousand-kernel weight (Li et al. 2015; Tian et al. 2017). Negative effects of *Rht-B1b*, *Rht-D1b* and *Rht8b* on FHB resistance have been reported by several authors (e. g. Miedaner and Voss 2008; Srinivasachary et al. 2009; Mao et al. 2010; Buerstmayr and Buerstmayr 2016) and were confirmed for *Rht-D1b* in this study (Chapter 2). Genotypes carrying *Rht-D1b* revealed on average 10.05 percentage points more disease symptoms than individuals carrying the wild type allele. Therefore, a strong negative association between FHB and plant height was detected in the bi-parental family ‘History × Rubens’ segregating for the locus *Rht-D1* (Chapter 2). The reinforcing effects on FHB severity of the dwarfing allele of *Rht-B1* and very likely also of *Rht-D1*, are directly caused by the mutated DELLA proteins that reduce the sensitivity to the growth promoting hormone GA, but also enhance Type 1 susceptibility to FHB in comparison to the wildtype alleles (Saville et al. 2012). In contrast to these dwarfing alleles, reduced resistance to FHB was not associated with *Rht24b* (Chapter 2) or STB (data not shown), but reduced plant height by 8.96 cm and explained 51 % of the genotypic variation. Thus, in the bi-parental family ‘Solitär × Bussard’, which segregated for the GA sensitive dwarfing locus *Rht24*, but fixed for the *Rht-B1* and *Rht-D1* wildtype alleles, no association between FHB and plant height was observed. As quantitative traits, plant height and FHB in bread wheat are regulated by a large number of small-effect QTL besides the *Rht* genes (Löffler et al. 2009; Buerstmayr et al. 2009; Mao et al. 2010; Reif et al. 2011; Griffiths et al. 2012; Würschum et al. 2015; McIntosh et al. 2017; Würschum et al. 2017a). In general, adverse effects on FHB resistance by small-effect QTL for plant height occur occasionally (e. g. Gervais et al. 2003; Paillard et al. 2004; Schmolke et al. 2005; Holzapfel et al. 2008). Thus, lines of short plant stature appeared to be less resistant. In this experiment, four and three small-effect QTL were detected for plant height and FHB resistance, respectively (Chapter 2). None of these QTL were co-localized. Notably, artificial inoculation was applied from above. Plant height might considerably affect FHB severity in case of natural infection. Passive resistance mechanisms have been assumed for tall plants, such as the different

microclimate in ear height, an enhanced distance of the ears to the soil, or different canopy structure (Mesterházy 1995; Mao et al. 2010). Nevertheless, Hilton et al. (1999) and Gosman et al. (2008) found no differentiation in relative humidity at ear level between wheat lines of different plant height, indicating that varying degrees of FHB resistance cannot be explained by the microclimate alone. The findings of this experiment confirm that reduced resistance to FHB is not commonly a cause of plant height *per se*, but rather a direct effect of GA-insensitive *Rht-1* alleles. This demonstrates that in breeding programs the choice of dwarfing genes must be carefully considered when improved FHB resistance is a relevant breeding goal and breeders must select the appropriate dwarfing source that may confer resistance. However, in a large panel of 1,110 worldwide winter wheat cultivars, 44 % of the varieties carrying *Rht24b* where also carrier of the *Rht-B1* or *Rht-D1* dwarfing alleles (Würschum et al. 2017a). This indicates that *Rht24b* is often used to further decrease plant height in combination with other semi-dwarfing alleles rather than replacing them.

THE POTENTIAL OF *FHB1* AND *FHB5* QTL FOR BREEDING PROGRAMS

FHB resistance as quantitative trait is regulated by mostly small-effect QTL. More than 200 resistance QTL have been mapped to date, but only few major QTL have been described (Buerstmayr et al. 2009). The most prominent are *Fhb1* and *Fhb5* (Buerstmayr et al. 2002, 2003). While being widely used in North America (Steiner et al. 2017), so far only the cultivar ‘Jaceo’ has been developed in Europe carrying *Fhb1b*, but was deleted from the French Recommended list shortly thereafter. One reason may be that the introgression of these non-adapted QTL also implies disadvantages through linkage drag. Von der Ohe et al. (2010) observed that the alleles *Fhb1b* and *Fhb5b* slightly negatively affect grain yield in backcross populations of two elite high-yielding cultivars. However, this adverse effect was significant only in one population and both loci might be appropriate QTL for counterbalancing the increased FHB susceptibility affected by the semi-dwarfing allele *Rht-D1b* in high-yielding environments. In a highly FHB susceptible background, *Fhb5b* alone was able to compensate the negative effect of *Rht-D1b* on FHB resistance, whereas *Fhb1b* could not counterbalance this negative impact (Chapter 3). Contrary to this result, Lu et al. (2011) announced that *Fhb1b* and *Fhb5b* are both necessary for counterbalancing the increased FHB susceptibility through *Rht-D1b*. This opens up the possibility of developing semi-dwarf wheat without reducing FHB resistance as molecular markers for *Fhb5* are available enabling the marker-assisted introgression of this locus (Buerstmayr et al. 2018). The result of this study is in accordance

with Von der Ohe et al. (2010), who also reported that *Fhb5b* affected FHB resistance to a higher extent than *Fhb1b*, though the difference was not significant in their study. The group further observed that in one backcross population the combination of *Fhb1b* + *Fhb5b* led to a significant loss of grain yield of 4 % while the progenies with *Fhb5b* alone yielded to the same extent as the progenies without any of these resistance alleles. Therefore, in practical wheat breeding programs, the utilization of the resistance allele of *Fhb5* would support the selection of semi-dwarf, FHB-resistant progenies and, thus, provide a valuable basis for the prospective development of cultivars. However, experiments reporting effects of *Fhb5* on important agronomic traits are limited to the study of von der Ohe et al. (2010). Studies investigating the effect of *Fhb5* in diverse genetic backgrounds are needed as they would evaluate the potential application in European breeding programs.

BREEDING PROGRESS BY GENOMIC SELECTION

When resistance to a disease is based on monogenic resistance, it puts high selection pressure on the respective pathogen to broken down resistance. Indeed, e. g. breeding history for STB has shown that resistance was readily overcome when achieved through one major QTL or gene alone (Ahmed et al. 1995; Jackson et al. 2000; McDonald and Linde 2002). Thus, durable resistance should be attained through the accumulation of native minor resistance QTL in combination with major QTL. However, conventional recurrent selection procedures aiming for this goal are time-consuming. GS might be the right tool to facilitate resistance breeding as it is possible to predict breeding values of a much larger number of genotypes than by visual scoring. Indeed, GS has been proven to be a powerful method for increasing the prediction accuracies for FHB and STB resistances in cross validation studies (Rutkoski et al. 2012; Arruda et al. 2015; Mirdita et al. 2015a and 2015b; Poland and Rutkoski 2016; Juliana et al. 2017a). Besides this approach, in this experiment, the potential of within- and among-family predictions was investigated, which is a much more realistic scenario of using GS in a plant breeding program (Wegenast et al. 2008; Würschum 2012). In accordance with previous findings, prediction accuracies achieved through cross-validation of a diversity panel were promising for FHB and STB resistances, plant height and heading date and increased with decreasing genetic complexity of the trait (Chapter 4; Rutkoski et al. 2012; Würschum et al. 2014; Arruda et al. 2015; Mirdita et al. 2015a and 2015b; Zhang et al. 2015; Michel et al. 2016; Poland and Rutkoski 2016; Juliana et al. 2017a; Würschum et al. 2017b). The prediction accuracies evaluated within individual families were lower than those across families (cross-

validation of a diversity panel) for all traits and differed between families likely due to varying population sizes, genetic architecture of the trait under investigation, as well as the number of segregating markers. The prediction accuracies among families were assessed by using one bi-parental family as training set and predicting another bi-parental family and were usually lower than prediction accuracies achieved within families. In general, prediction accuracies were higher between half-sib families than between unrelated bi-parental populations. In line with these observations, studies have been shown that better prediction results are caused by a higher average kinship between validation and training population (Lehermeier et al. 2014; Lorenz and Smith 2015; Han et al. 2016; Würschum et al. 2017b). Especially shared major QTL like *Rht-D1* between populations had a considerable influence on enhancing the prediction accuracy (Chapter 4). In this study, furthermore, the impact of two different GS models on prediction accuracy was examined. The first model was the commonly used RR-BLUP method, considering all markers as random effects. The second prediction model was wRR-BLUP, which assumes significant markers as fixed effects and all remaining markers as random effects. Significant markers were detected by a genome-wide association scan (GWAS) as proposed by Spindel et al. (2016). The upweighting of significant markers improved prediction accuracies when large-effect QTL were present (Bernardo 2014; Rutkoski et al. 2014; Zhao et al. 2014; Arruda et al. 2016; Boeven et al. 2016; Losert et al. 2016; Spindel et al. 2016; Juliana et al. 2017b; Moore et al. 2017; Michel et al. 2018). In accordance with these results, this work suggests that prediction accuracies for heading date, plant height, FHB and STB resistances in wheat can be enhanced by the utilization of prior information about QTL-targeted markers. Hence, the wRR-BLUP model should be the preferred GS model. Indeed, the incorporation of QTL, identified by the GWAS, into the model led to considerable increases of prediction accuracy. Strong improvements of prediction accuracy especially occurred when conducting cross-validation in individual families and by predicting one segregating family to another segregating family. However, the fixed model approach decreased the prediction accuracy in comparison to the full random model method in some prediction constellations. This only occurred when the prediction accuracy yielded by a full random model was already low (Chapter 4) and is likely the consequence of the incorporation of inaccurate markers which are not important in the validation set or due to epistasis (Spindel et al. 2016; Michel et al. 2018). For low heritable traits like grain yield, significant marker-trait associations are often not repeatable across years even in large mapping populations (He et al. 2016a) and modelling them as fixed effects might thus introduce an error putatively decreasing the prediction accuracy (Michel et al. 2018). In this study, however, the usage of a fixed model was never

disadvantageous when the prediction accuracies were already moderate to high, indicating that this approach should be the method of choice (Chapter 4). The results of this study illustrate that GS can be used for predictions within bi-parental families and within gene pools, which represent the germplasm of a breeding program. However, the prediction accuracies within families differed considerably between the cross-validation runs, illustrating that the composition of the training set is a crucial factor for the correct calculation of genomic estimated breeding values (GEBVs). So far, it appears to be not possible to identify a superior training population based on marker data solely (Marulanda et al. 2015). Predictions from one family to another seem less beneficial in unrelated and even half-sib families.

REALIZED GAIN FROM GENOMIC SELECTION

The majority of recent studies present the success of GS as estimation of prediction accuracy, but this method, does not represent the circumstances in plant breeding programs. While the prediction accuracy is an useful indicator for the performance of a model, it does not reply to the most urgent questions of a breeder: What is the percentage of the top individuals correctly selected for a given trait? Is it possible to select breeding parents based on their GEBVs? How much realized selection gain can be achieved by the GS approach? Hence, predictions must be validated in critical experiments. So far, there have been only a few studies reporting realized gain from GS in wheat and maize and none for FHB or STB resistances (Combs and Bernardo 2013; Massman et al. 2013; Beyene et al. 2015; Rutkoski et al. 2015; Michel et al. 2017). Combs and Bernardo (2013) found that GS led to better mean performance of grain yield in maize compared with phenotypic backcrossing. Massman et al. (2013) reported that GS provided superior response for stover yield and grain yield and stover indices by 14 to 50 % over marker-assisted recurrent selection in a bi-parental temperate maize population. Beyene et al. (2015) announced that GS yielded higher genetic gains for tropical maize grain yield under drought stress in comparison to a pedigree-based conventional phenotypic selection (PS). Rutkoski et al. (2015) and Michel et al. (2017) found gain from GS to be similar to gain from PS for stem rust in spring wheat and wheat grain yield in winter wheat, respectively. In this study, the GEBVs of 2,500 untested genotypes were calculated based on a partially related training population of 1,120 genotypes. The most resistant FHB and STB individuals were genetically selected in comparison to a random sample under consideration of plant height. A main breeding goal in Middle Europe is semi-dwarf wheat, however, a strong negative association between FHB resistance and plant height was observed (Chapter 5). Therefore, in this study a

moderate culling level of 96.93 cm representing the average GEBVs for plant height of the whole validation population plus 5 % was applied to avoid the selection of too tall genotypes that are not accepted by agronomic practice. For FHB resistance, a genomic selection advantage of 10.62 percentage points in comparison to the random sample was achieved, indicating that GS is a promising approach for that trait (Chapter 5). However, GS failed to improve resistance to STB and the coefficient of correlation between predicted and observed FHB severity was 4.8 times higher than for STB severity. These results are in accordance with Mirdita et al. (2015b), who reported a three times larger prediction accuracy for FHB than for STB resistance in an independent validation study when predicting a less related test set. Stable and high prediction trait accuracies are apparently preferable, however, when high genotype-by-environment interactions are present, accurate predictions are difficult to attain. Promising prediction accuracies for STB resistance achieved in cross-validation studies so far (Mirdita et al. 2015a; Juliana et al. 2017a) are likely a result from overestimation as genotypes from the training population and validation population are tested in the same environment (Storlie and Charmet 2013; Krchov et al. 2015). Indeed, the heritability of STB was lower than that of FHB, because of a strong genotype-by-location interaction variance explaining the highest proportion of variation for that trait as a result of highly differing weather conditions between locations and the much higher demand of STB for humidity during inoculation compared to FHB (Chapter 5). This makes the use of GS for STB resistance even more challenging. In plant breeding programs, the appropriate selection of the most promising genotypes for advanced field trials is a crucial factor for the successful development of cultivars. It is further an urgent question of a plant breeder, whether it is possible to select superior breeding parents by GS as it is already a standard procedure in livestock breeding (Hayes et al. 2009). The identification of crossing parents based on GEBVs in early generations would lead to shorter breeding cycles, because it would not be longer necessary to wait for higher generations to phenotype quantitative traits (Heffner et al. 2009; Bassi et al. 2016; Poland and Rutkoski 2016). The results of this study indicate that the selection of breeding parents based on GEBVs for high FHB resistance seems not to be sufficiently reliable as the percentage of correctly genetically selected individuals among the observed 10 % top individuals for the whole selection population was only 19 %. However, Michel et al. (2017) reported that the possibility of selecting the best performing lines was much higher by GS than by conventional PS for grain yield in wheat for advanced field trials in several environments.

THE IMPLEMENTATION OF GENOMIC SELECTION INTO BREEDING PROGRAMS

GS has been proposed as valuable breeding tool for traits controlled by many QTL of predominantly small effects. Hence, quantitative FHB and STB resistances appear to be appropriate target traits. Many suggestions about the implementation of GS into breeding programs have been made as its broad application possibilities allow different strategies (Heffner et al. 2009, 2010; Nakaya and Isobe 2012; Longin et al. 2015; Rutkoski et al. 2015; Bassi et al. 2016; Marulanda et al. 2016; Poland and Rutkoski 2016; Spindel et al. 2016). In general, it is assumed that GS is conducted in early generations of a breeding scheme before applying advanced field trials. Breeders can, therefore, consider the reduction of traditional field trials by GS to save phenotyping costs (Endelman et al. 2014). Two possible GS implementation scenarios into a wheat breeding program based on double haploid technique are shown in Figure 3. The breeding cycle begins with the identification and intermating of inbred parents taking into account all desired target traits. From their crossing offspring (F_1) double haploid plants (D_0) are developed. These plants are genotyped and a GS model is applied for the prediction of their GEBVs for all target traits including necessary single genes, like *Rht* and photoperiod response (*Ppd*) alleles. Two scenarios are conceivable: In the breeding scheme A, culling of the worst performing genotypes takes place. In breeding scheme B, new crossing parents are selected based on GEBVs. However, in this study the percentage of correctly genetically selected top individuals for FHB resistance was only 19 % and failed for STB resistance (Chapter 5) and, thus, evidence is required to test for the efficiency of GS for the selection of new breeding parents and the applicability of breeding scheme B. In both breeding schemes, all sets of genetically positive selected D_1 seeds, each derived from one D_0 plant, are planted in single rows at two to three locations for selection of highly heritable traits. Generation D_2 and D_3 are phenotyped in replications and multi-location wise for grain yield, baking quality and other low-heritable traits and genotyped, because their trait values are used to update the GS model for all measured traits. In generation D_4 already the first year of testing the value for cultivation and use takes place. Each stage in the breeding pipeline is characterized by a decrease in the overall number of genotypes and increase in the level of field testing. In breeding scheme A, new crossing parents are phenotypically selected based on generation D_2 and D_3 . These two GS applications are applicable for all target traits and the application of GS in early breeding cycles makes it especially attractive for traits which are normally tested in later generations. Some traits like FHB and STB resistances (Chapter 4 and 5, Jiang et al. 2014; Mirdita et al. 2015a, 2015b) or frost tolerance (Sieber et al. 2014; Sieber et al. 2016) cannot be

observed every year and special tests are necessary. GS might further greatly support selection for abiotic stress tolerances like drought or heat stress, when large, adequate training populations are available. Otherwise, such traits must be phenotyped under special labor- and cost-intensive conditions in higher generations (Ziyomo and Bernardo 2013; Beyene et al. 2015; Vivek et al. 2016). Thus, GS gives the potential of selecting lines with desired traits in early breeding generations showing better yield stability under biotic and abiotic stress conditions in the future (Wang et al. 2015; Huang et al. 2016). Here, the GS model under application must be considered. In this study, wRR-BLUP has shown to be an effective method for FHB resistance, plant height and heading date (Chapter 4 and 5). However, this model failed to improve resistance to STB. The year 2018 in which the selection population was tested, was the warmest year since begin of weather records with extremely low precipitation (DWD 2018) making successful inoculation with STB more challenging and causing strong genotype × environment interactions (GE). These conditions might be one reason why GS was less effective for STB than for FHB resistance. An alternative method for traits with strong GE is the incorporation of the respective effects into the prediction model to increase accuracy (Zhang et al. 2015). Modeling epistatic effects might further provide a significant advantage (Jiang and Reif 2015, Mirdita et al. 2015b). Mirdita et al. (2015b) yielded higher prediction accuracies for STB resistance in comparison to RR-BLUP when applying an extended genomic best linear unbiased prediction model which explicitly modeled epistasis (EG-BLUP; Jiang and Reif 2015) or reproducing kernel Hilbert space regression (RKHSR; Gianola et al. 2006), which also captures epistatic effects among markers (Gianola and van Kaam 2008; Morota and Gianola 2014; Jiang and Reif 2015). Additionally, a crucial factor for maintaining high prediction accuracies is a high degree of relatedness between validation and training set (Asoro et al. 2011; Nakaya and Isobe 2012; Lehermeier et al. 2014; Lorenz and Smith 2015; Han et al. 2016; Würschum et al. 2017b). This study has shown that predictions among families appear to be not reliable, even in half-sib families, while predictions within families were a more promising approach (Chapter 5) as recently also reported by Würschum et al. (2017b). Moreover, breeders broaden their breeding pools by the steadily introgression of foreign plant material (Sallam et al. 2015; He et al. 2016b; Michel et al. 2017). This leads to an uncertain structure of the breeding populations. Simulation studies (Habier et al. 2013) and empirical experiments (Lorenz and Smith 2015) investigated the effects on the prediction accuracy when distant relatives are added to the GS models. The results explicitly illustrate a decrease of prediction accuracy with declining degree of relatedness. Thus, GS might be a useful tool to predict traits within bi-parental populations (Lorenzana and Bernardo 2009; Heffner et al. 2011; Krchov and Bernardo

2015). By applying GS, the number of individuals could be enhanced enabling an increase of selection intensity given that GS is cheaper than phenotypic evaluation. When foreign germplasm was integrated into the breeding program which is currently not present in the training population, each bi-parental family could be parted into one fraction to be phenotyped and genotyped forming the training population and one fraction to be genotyped only and predicted as validation population. The advantage of this approach is represented by the low marker density needed as extensive linkage disequilibrium enables genome-wide marker coverage to be achieved with little expense in wheat (Jannink et al. 2010; Heffner et al. 2011). However, an unfavorable effect is the extension of the breeding cycle as the first generation of offspring needs to be phenotyped before performing GS. Hence, a multifamily GS approach that uses predictions from a training population consisting of advanced breeding lines from many families that have passed the breeding program would be preferable as described above.

In conclusion, several opportunities how to implement GS into a breeding program do exist and it is mainly a decision of management, the cost-benefit ratio, and the priorities of the respective breeder. Moreover, a crucial factor determining long-term response to selection is the maintaining of genetic diversity in a breeding program (Cowling 2013). GS has shown to provide similar gain as phenotypic selection but resulted in a significantly higher reduction of genetic variance especially at loci with large effect (Rutkoski et al. 2015; Sallam and Smith 2016). Therefore, experiments investigating long-term response to genomic selection are urgently required to support breeder's decisions.

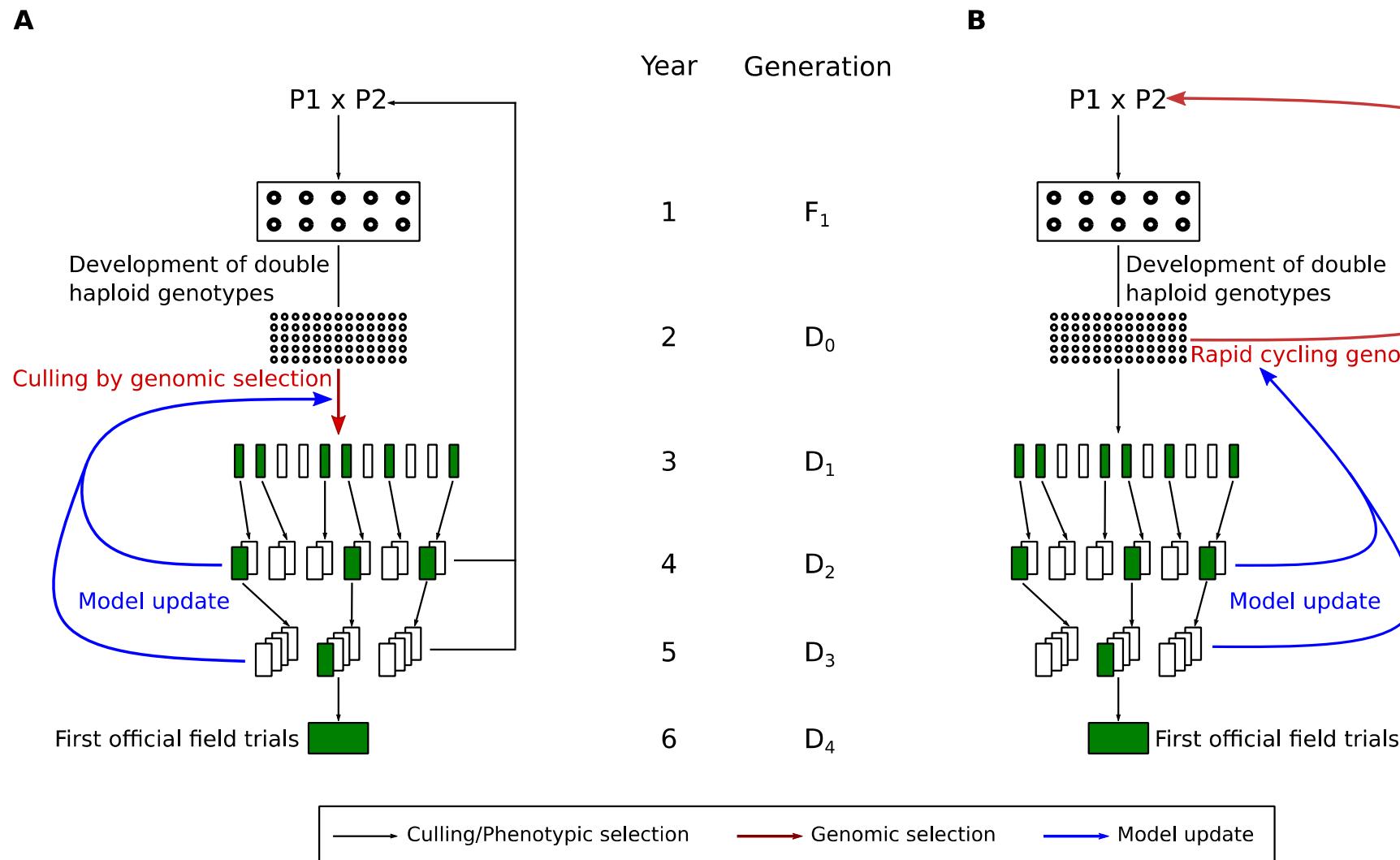


Fig. 3 Breeding scheme of winter wheat under application of double haploid technique and genomic selection (GS). Two possible implementation steps of GS are illustrated. **A** GS either is applied for culling the worst performing D₀ individuals or **B** to identify new breeding parents.

7 SUMMARY

Fusarium head blight (FHB) and Septoria tritici blotch (STB) are devastating cereal diseases reducing quality and yield in Central Europe. As both traits are predominantly quantitatively inherited, resistant cultivars are developed by the accumulation of quantitative trait loci (QTL). Conventional recurrent selection procedures aiming for this goal are labor- and time-consuming. Furthermore, resistance breeding is complicated by the long latent period of STB, a great variability of the pathogen populations and a negative association between reduced height (*Rht*) genes and both diseases. The resistance breeding progress could be supported by the utilization of major QTL in addition to minor QTL. Indeed, the non-adapted major FHB resistance QTL *Fhb1* and *Fhb5*, derived from Chinese wheat, have been successfully implemented in North American breeding programs. In European companies, however, these QTL are not currently used. *Rht* loci that provide the agronomical important short plant stature without adverse effects on FHB and STB resistances are further urgently required. As alternative strategy to pure phenotypic selection, genomic selection (GS) has been proposed to facilitate breeding progress. This method enables the prediction of trait values of a much larger number of genotypes at lower costs than by visual scoring. Several studies have demonstrated the potential of GS to increase prediction accuracy of FHB and STB resistances in cross-validation studies. Experiments investigating the potential of genomic selection across different populations and its success for improving disease resistance are lacking. Hence, the aims of this study were to improve selection for FHB and STB resistances by (i) evaluating the effect of the recently described dwarfing locus *Rht24* in comparison to the widely used *Rht-D1* on FHB and STB resistances, plant height, and heading date for the first time, (ii) investigating the potential of the non-adapted QTL *Fhb1* and *Fhb5* for breeding semi-dwarf wheat, (iii) analyzing the prediction accuracy achieved by within- and among-family prediction comparing the models ridge regression-best linear unbiased prediction (RR-BLUP) and weighted RR-BLUP (wRR-BLUP), and (iv) computing the advantage from genomic selection and determine the percentage of correctly selected top 10 % individuals for FHB and STB resistances.

The results of this study demonstrated that the most recently described gibberellic acid sensitive dwarfing gene *Rht24* on chromosome 6A reduces plant height by 8.96 cm without adverse effects on FHB and STB resistances. Further, no association with heading date was observed. In contrast, *Rht-D1b* decreased FHB resistance by 10.05 percentage points. This work has further shown, that the resistance alleles of *Fhb1* and *Fhb5* reduced FHB severity by 6.54 and 11.33 percentage points, respectively, and that the non-adapted allele *Fhb5b* alone was able to

counterbalance the negative impact of *Rht-D1b* on FHB resistance in a population consisting of eight bi-parental families segregating for these resistance loci. This indicates that in breeding programs the choice of semi-dwarfing and FHB resistance genes is of crucial importance where improvement of FHB resistance is a relevant breeding goal and breeders must select the appropriate dwarfing source that may confer resistance. In this study, furthermore, the potential of GS within and among families was investigated. The prediction accuracies evaluated within individual families were higher than those among families for all traits and differed between families and prediction constellations. The upweighting of significant markers by using the wRR-BLUP model was superior to the commonly used RR-BLUP model when large effect loci like *Rht-D1* or *Fhb5* were present. In this study, the genomic estimated breeding values (GEBVs) of 2,500 untested genotypes were calculated based on a partially related training population of 1,120 genotypes and the 10 % most resistant FHB and STB individuals were selected as well as a random sample under consideration of plant height. The best linear unbiased estimators (BLUES) of the selected genotypes were evaluated at four ecologically different locations relative to a randomly selected sample of genotypes. For FHB resistance, a genomic selection advantage of 10.62 percentage points relative to the random sample was achieved. However, GS improved resistance to STB only by 2.14 percentage points. The results of this study indicate that a rigorous selection of breeding parents based on GEBVs for high FHB resistance seems not to be sufficiently reliable as the percentage of correctly selected individuals of the observed 10 % top individuals for the whole selection population was only 19 %.

In summary, GS has shown to be a valuable tool to support the breeding progress for the complex inherited FHB resistance over short cycles and increased population sizes. Increased resistance to FHB in winter wheat could be achieved by that approach in combination with the choice of the appropriate dwarfing source and the potential use of the non-adapted QTL *Fhb5*.

8 ZUSAMMENFASSUNG

Ährenfusarium (FHB) und die Septoria-Blattdürre (STB) sind verheerende Getreidekrankheiten, die in Mitteleuropa zu erheblichen Qualitäts- und Ernteverlusten führen können. Da beide Krankheiten überwiegend quantitativ vererbt werden, können resistente Sorten durch die Akkumulation von QTL (*quantitative trait loci*) entwickelt werden. Dies kann durch rekurrente Selektion erreicht werden, die jedoch zeit- und arbeitsintensiv ist. Zusätzlich wird die Resistenzzüchtung durch die lange Latenzperiode von STB, eine große Variabilität der Pathogenpopulationen und einem negativen Zusammenhang zwischen *Reducing height (Rht)*-Genen und Resistzenzen erschwert. Eine zusätzliche Nutzung von Major-QTL könnte den Zuchtfortschritt unterstützen. In Nordamerika wurden dafür *Fhb1* und *Fhb5* aus chinesischem Weizen bereits erfolgreich genutzt. Europäische Unternehmen haben diese QTL bisher nicht in ihr Zuchtmaterial implementiert. *Rht*-Gene, die die agronomisch notwendige Kurzstrohigkeit bewirken und dabei die FHB- und STB-Resistzenzen nicht mindern, werden zusätzlich dringend benötigt. Die genomische Selektion (GS) stellt eine Alternative zur reinen phänotypischen Selektion dar und ihre Anwendung ermöglicht eine Beschleunigung des Zuchtfortschritts, da diese Methode die Vorhersage von Selektionsmerkmalen einer größeren Anzahl von Genotypen ermöglicht als phänotypisch im Feldversuch getestet werden könnte. Mehrere Kreuzvalidierungsstudien haben gezeigt, dass die GS das Potenzial trägt, die Vorhersagegenauigkeit (*prediction accuracy*) für FHB- und STB-Resistzenzen zu erhöhen. Experimente, die das Potential der GS für die Vorhersage zwischen verschiedenen Populationen und den genomischen Selektionsgewinn untersuchen, beschränken sich bisher auf wenige Studien. Daher waren die Ziele dieser Arbeit (i) die erstmalige Evaluierung des Effekts des Zergengens *Rht24* auf FHB- und STB-Resistzenzen, Wuchshöhe und Ährenschieben im Vergleich zum weit genutzten Locus *Rht-D1*, (ii) die Untersuchung des Potenzials der nicht-adaptierten QTL *Fhb1* und *Fhb5* für die Entwicklung von Kurzstrohweizen, (iii) die Analyse der Vorhersagegenauigkeit von GS innerhalb und zwischen Familien durch die Anwendung der beiden Modelle RR-BLUP (*ridge-regression best linear unbiased prediction*) und wRR-BLUP (*weighted RR-BLUP*) und (iv) die Berechnung des Selektionsgewinns bzw. die Bestimmung der korrekt selektierten Top-10 %-Genotypen für FHB- und STB-Resistzenzen durch GS.

Die Ergebnisse dieser Studie zeigten, dass das gibberellinsäuresensitive Zergen *Rht24* auf Chromosom 6 die Wuchshöhe um durchschnittlich 8,96 cm senkte, ohne dabei die FHB- und STB-Resistzenzen oder den Zeitpunkt des Ährenschiebens ungünstig zu beeinflussen. Demgegenüber senkte das weitläufig verwendete Allel *Rht-D1b* die FHB-Resistenz um

durchschnittlich 10,05 Prozentpunkte in einer Winterweizenpopulation bestehend aus acht biparentalen Familien, die für diese Resistenzloci segregierten. Diese Arbeit hat zusätzlich aufgezeigt, dass die Resistenzallele von *Fhb1* und *Fhb5* die FHB-Anfälligkeit um 6,54 bzw. 11,33 Prozentpunkte reduzierten und somit bereits allein das nicht-adaptierte Allel *Fhb5b* in der Lage ist, den negativen Effekt von *Rht-D1b* auf die FHB-Resistenz im untersuchten Material auszugleichen. Das verdeutlicht, dass die Wahl der Zwerp- und Resistenzgene in Zuchtprogrammen, in denen FHB-Resistenz ein Selektionsmerkmal ist, von entscheidender Bedeutung ist. In dieser Studie wurde des Weiteren das Potenzial der GS innerhalb und zwischen Familien untersucht. Die Vorhersagegenauigkeiten innerhalb einer Familie waren für alle Zielmerkmale höher als die zwischen Familien und unterschieden sich zwischen den einzelnen Familien und Vorhersagekonstellationen. Die stärkere Gewichtung von signifikanten Markern durch das wRR-BLUP-Modell führte zu einer Verbesserung der Vorhersagegenauigkeit im Vergleich zum weit genutzten RR-BLUP-Modell, wenn einzelne Gene, wie *Rht-D1*, oder Major-QTL, wie *Fhb5*, vorhanden waren. In dieser Studie wurden die genomisch geschätzten Zuchtwerte (GEBVs) von 2.500 ungeprüften Genotypen bestimmt, basierend auf einer partiell verwandten Trainingspopulation von 1.120 Genotypen. Die 10 % FHB- und STB-resistentesten Linien und eine zufällige Stichprobe wurden unter Berücksichtigung der Wuchshöhe genomisch selektiert und phänotypisch in einem vierortigen Feldversuch evaluiert. Für die FHB-Resistenz wurde ein Selektionserfolg von 10,62 Prozentpunkten relativ zur zufällig selektierten Populationsstichprobe ermittelt. Die GS erhöhte die STB-Resistenz allerdings nur um 2,14 Prozentpunkte. Auch die Selektion von neuen Kreuzungseltern auf der Basis von GS erscheint nicht ausreichend zuverlässig, da nur 19 % der Top-10 %-Individuen korrekt selektiert wurden.

Zusammenfassend stellt die GS ein wertvolles Werkzeug dar, um den Zuchtfortschritt für die komplex vererbte FHB-Resistenz über kürzere Zyklen und größere Populationen zu unterstützen. In Kombination mit der Nutzung geeigneter Zwerggene und des nicht adaptierten QTL *Fhb5* kann dadurch eine Steigerung der FHB-Resistenz im Winterweizen erzielt werden.

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ACKNOWLEDGEMENTS

First of all, I would like to thank Prof. Dr. Thomas Miedaner for giving me the possibility to do my PhD at the State Plant Breeding Institute, his support and advice during this thesis and always having an open door for all my matters of importance.

I would like to express my gratitude to Bärbel and Marlene for their support and engagement. I could always rely on your help – at any time in any situation. Many thanks!

I like to thank our project partners Dr. Sonja Kollers, Dr. Erhard Ebmeyer and Dr. Viktor Korzun for the rich exchange and the helpful feedback.

I further thank all the technical and laboratory staff of the State Plant Breeding Institute, and all members of the experimental stations Heidfeldhof, Oberer Lindenhof, Wetze and Wohlde for the excellent conductance of the field trials and the lab analyses building the very basis that made this thesis possible.

I also like to thank Tobias and Willmar for their suggestions and ideas during the development of my papers.

My special thanks go to Alena. It was a great time sharing an office, my sorrows and joys with you.

I further express my gratitude to Anna, Felix, Paul and Valheria.

Finally, I want to thank Jonas for his tremendous support during my entire study time.

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DECLARATION

Eidesstattliche Versicherung

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

1. Bei der eingereichten Dissertation zum Thema
**„Prospects of genomic selection for disease resistances in winter wheat
(*Triticum aestivum L.*)“**
handelt es sich um meine eigenständig erbrachte Leistung.
2. 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.
3. Ich habe nicht die Hilfe einer kommerziellen Promotionsvermittlung oder -beratung in Anspruch genommen.
4. 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.

Ort und Datum

Unterschrift

Eidesstattliche Versicherung Belehrung

Die Universität Hohenheim verlangt eine Eidesstattliche Versicherung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistungen, um sich glaubhaft zu versichern, dass die Promovendin bzw. der Promovend die wissenschaftlichen Leistungen eigenständig erbracht hat.

Weil der Gesetzgeber der Eidesstattlichen Versicherung eine besondere Bedeutung beimisst und sie erhebliche Folgen haben kann, hat der Gesetzgeber die Abgabe einer falschen eidesstattlichen Versicherung unter Strafe gestellt. Bei vorsätzlicher (also wissentlicher) Abgabe einer falschen Erklärung droht eine Freiheitsstrafe bis zu drei Jahren oder eine Geldstrafe.

Eine fahrlässige Abgabe (also Abgabe, obwohl Sie hätten erkennen müssen, dass die Erklärung nicht den Tatsachen entspricht) kann eine Freiheitsstrafe bis zu einem Jahr oder eine Geldstrafe nach sich ziehen.

Die entsprechenden Strafvorschriften sind in § 156 StGB (falsche Versicherung an Eides Statt) und in § 161 StGB (Fahrlässiger Falscheid, fahrlässige falsche Versicherung an Eides Statt) wiedergegeben.

§ 156 StGB: Falsche Versicherung an Eides Statt

Wer vor einer zur Abnahme einer Versicherung an Eides Statt zuständigen Behörde eine solche Versicherung falsch abgibt oder unter Berufung auf eine solche Versicherung falsch aussagt, wird mit Freiheitsstrafe bis zu drei Jahren oder mit Geldstrafe bestraft.

§ 161 StGB: Fahrlässiger Falscheid, fahrlässige falsche Versicherung an Eides Statt

Abs. 1: Wenn eine der in den §§ 154 und 156 bezeichneten Handlungen aus Fahrlässigkeit begangen worden ist, so tritt Freiheitsstrafe bis zu einem Jahr oder Geldstrafe ein.

Abs. 2: Straflosigkeit tritt ein, wenn der Täter die falsche Angabe rechtzeitig berichtigt. Die Vorschriften des § 158 Absätze 2 und 3 gelten entsprechend.

Ich habe die Belehrung zur Eidesstattlichen Versicherung zur Kenntnis genommen.

Ort und Datum

Unterschrift