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Sélection d'un Triticale à faible teneur en mycotoxin

par Marine OLLIER

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BREEDING OF A LOW MYCOTOXIN TRITICALE

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ABSTRACT

Fusarium head blight (FHB) is a cereal disease of major importance responsible for yield losses and mycotoxin contaminations in grains. Here we characterized the resistance to FHB in triticale breeding material harboring resistance factors from bread wheat. Additionally, we introduce a new measurement approach to quantify FHB severity on grains based on the evaluation of the whitened kernel surface (WKS) using digital image analysis. A highly FHB resistant experimental line which derives from a triticale × wheat cross was crossed to several modern triticale cultivars to generate three triticale populations. These mapping populations were phenotyped for Fusarium head blight resistance in replicated field trials under artificial inoculation and were genotyped with genotyping-by-sequencing (GBS) and SSR markers. FHB severity was assessed in the field by visual scorings and on the harvested grain samples by a digital evaluation of the WKS. Aside from this breeding work, the applicability of WKS was assessed on two bread wheat and one triticale grain sample sets with 265 samples in total. Pearson correlation coefficients between Fusarium-damaged kernels (FDK) and WKS range from r = 0.77 to r = 0.81 and from r = 0.61 to r = 0.86 for the correlation between deoxynivalenol (DON) content and WKS. As a low-cost and fast approach, this method appears particularly attractive for breeding and genetic analysis of FHB resistance where typically large numbers of experimental lines need to be evaluated, and for which WKS is suggested as an alternative to visual FDK scorings. Four QTL with major effects on FHB resistance were identified in our three mapping populations. They map to chromosomes 2B, 3B, 5R and 7A. The QTL on 3B collocated with Fhb1 and the QTL on 5R with the dwarfing gene Ddw1. This is the first report demonstrating the successful introgression of Fhb1 into triticale which comprises a significant step forward for enhancing FHB resistance in this crop.

RÉSUMÉ

La fusariose de l'épi (FHB) est une maladie des céréales d'importance majeure susceptible de générer des pertes de rendement et de contaminer les récoltes avec des mycotoxines. Notre projet vise à caractériser la résistance génétique à la fusariose chez le triticale et plus particulièrement à évaluer l'impact de l'introgression de facteurs de résistance du blé panifiable chez le triticale. En complément, une nouvelle approche de quantification des symptômes de la fusariose sur grains a été développée. Cette approche est basée sur une évaluation digitale de la surface de grain blanchie (ou WKS pour Whitened Kernel Surface). Une lignée hautement résistante à la fusariose, issue d'un croisement triticale × blé, a été croisée avec plusieurs cultivars de triticales modernes pour générer trois populations distinctes. Ces populations ont été génotypées par marqueurs microsatellites (SSR) ainsi qu'à l'aide de marqueurs obtenus par séquençage (GBS). Le phénotype pour la résistance à la fusariose a été obtenus au champ lors de multiples essais en conditions répliquées et sous inoculation artificielle. La sévérité de la fusariose a été évaluée par une notation visuelle des épis au champ et par une évaluation digitale de la WKS des grains après la récolte. En complément de ce travail de sélection variétale, l'applicabilité de WKS a été évaluée sur deux lots d'échantillons de blé tendre et un lot de triticale pour 265 échantillons au total. Les coefficients de Pearson entre l'évaluation visuelle des symptômes sur grains (ou FDK pour Fusarium Damaged Kernels) et la WKS vont de r = 0,77 à r = 0,81 et de r = 0,61 à r = 0,86 pour ceux entre la teneur en déoxynivalénol (DON) et la WKS. A la fois rapide et peu coûteuse, cette nouvelle méthode de quantification des symptômes sur grains semble particulièrement indiquée pour la sélection variétale et l'analyse génétique de la résistance à la fusariose. Ces pratiques nécessitent en effet l'évaluation du niveau d'infection d'un grand nombre d'échantillons, et dans ce contexte, la WKS se présente comme une alternative efficace à la notation visuelle FDK. Quatre QTL ayant des effets majeurs sur la résistance à la fusariose ont été identifiés au sein de nos trois populations de triticale, sur les chromosomes 2B, 3B, 5R et 7A. Le QTL sur le chromosome 3B colocalise avec *Fhb1* et celui sur le chromosome 5R avec le gène de nanisme *Ddw1*. Il s'agit de la première démonstration d'une introgression réussie de *Fhb1* dans plusieurs fonds

génétiques de triticale, ce qui constitue une avancée majeure dans l'amélioration de la résistance à la fusariose chez cette espèce.

ZUSAMMENFASSUNG

Fusarienkopfschädling (FHB) ist eine Getreidekrankheit, die hauptsächlich für Ertragsverluste und Mykotoxinkontamination in Getreide verantwortlich ist. In dieser Arbeit wurde die Resistenz von Triticale-Zuchtmaterial mit Resistenzfaktoren von Brotweizen gegen FHB charakterisiert. Darüber hinaus basiert der FHB-Schweregrad von Körnern, unter Verwendung der digitalen Bildanalyse, auf der Bewertung der Oberfläche des weißen Kerns (WKS). Dafür wurde eine hoch FHB-resistente experimentelle Linie, welche aus einer Triticale × Weizen-Kreuzung hervorging und aus mehreren modernen Triticale-Sorten abgeleitet ist, verwendet. Dadurch wurden drei Triticale-Populationen zu erzeugt. Diese Kartierungspopulationen wurden in replizierten Feldversuchen, unter künstlicher Inokulation, auf Resistenz gegen Fusarium-Kopfschädlinge phänotypisiert und mittels Genotypisierung durch Sequenzierung (GBS) und SSR-Markern genotypisiert. Die Bewertung des Schweregrads der FHB im Feld wurde an den geernteten Getreideproben durch visuelle und digitale Auswertung der WKS durchgeführt. Abgesehen von dieser Züchtungsarbeit, wurde die Anwendbarkeit von WKS an zwei Weizen- und einem Triticale -Probensätzen mit insgesamt 265 Proben evaluiert. Die Pearson-Korrelationskoeffizienten zwischen Fusarium-geschädigten Körnern (FDK) und WKS ist in einem Bereicht von r = 0,77 bis r = 0,81 und zwischen Deoxynivalenol (DON) -Gehalt und WKS von r = 0,61 bis r = 0,86. Als kostengünstiger und naheliegender Ansatz wird diese Methodik als Alternative zum visuellen FDK-Scoring verwendet. In den drei Kartierungspopulationen konnten vier QTL mit Hauptwirkungen auf die FHB-Resistenz identifiziert werden und liegen auf den Chromosomen 2B, 3B, 5R und 7A ab. Der QTL auf 3B kollokiert mit *Fhb1* und der QTL auf 5R mit jenen des Zwerggens *Ddw1*. Dies ist die erste Arbeit welche die erfolgreiche Introgression von *Fhb1* in dieser Kultur und ist somit ein großer Schritt vorwärts für die Weiterentwicklung von FHB-Resistenz in Triticale.

GENERAL INTRODUCTION

Triticale: Overview on a man-made crop

Origin and cytogenetics

Triticale (*Triticosecale Wittmack*) is the intergeneric amphidiploid between the female parent wheat (*Triticum ssp.*) and the male parent rye (*Secale ssp.*). The first report describing the production of hybrid plants between wheat and rye was presented by Wilson in 1875 to the Botanical society of Edinburgh, Scotland (Wilson, 1976). Those plants were completely sterile, and partially fertile hybrids only arose later in the 19th century. At that time there was a very limited interest for breeding. The main drawbacks were the tendency to lodge, susceptibility to sprouting, and low yield potential, mostly due to partial sterility (FAO, 2004). A significant breakthrough came in the 1930s with the use of colchicine as a diploidization reagent (Blakeslee & Avery, 1937). The development of this technology marked the true start of triticale breeding with the first commercial varieties released in the 1970s (FAO, 2004). Breeding efforts were first orientated toward the development of octoploid triticale, combining the rye genome (R) with the hexaploid (ABD) wheat genome. However, due to superior vigor and yield stability, all modern commercial varieties are now hexaploidy triticale (Cheng & Murata, 2002; Fox et al., 1990; Lukaszewski & Gustafson, 1987). They combine the rye genome with the tetraploid wheat (AB) genome, having a genomic constitution of AABBRR with 2n = 6x = 42 chromosomes (Oettler et al., 2005). Lines generated from wheat x rye crosses are termed 'primary triticale', while lines selected from triticale x triticale crosses are called 'secondary triticale'. Triticale cultivars exist as winter and spring types. Spring triticales are grown across five continents, while winter triticales are concentrated in Northern Europe and North America.

Utilization & Economic importance

The initial interest of crossing wheat and rye was the potential to combine the attributes of both cereals into a unique high-yielding crop that could be grown on marginal land under limited soil fertility and moisture (FAO, 2004; Hao et al., 2013; Mergoum et al., 2009). As a result, modern triticales are considered as low input cereal, which require lower fertilizer and crop protection measures compared to barley or wheat (FAO, 2004). Thanks to its extensive root system, triticale is particularly suited for marginal environments suffering from abiotic stresses and has shown high levels of disease resistance (FAO, 2004). The original intention for the development of triticale was production of human food. Although the nutritional content indicates high quality, this has not been a major use of the crop. Triticale show great potential in bio-fuels (ethanol), organic and industrial chemicals, paper, building and plastic industries and the beverage (beer) industry. However, those market segments remain marginal and most of the produced grain is still used on-farm as a feed grain (Bassu et al., 2011; Estrada-Campuzano et al., 2012; FAO, 2004; Fernández-Fígares et al., 2008; Glatthar et al., 2005; Gowda et al., 2011; Martinek et al., 2008; Mcgoverin et al., 2011; Rakha et al., 2011). The evolution of triticale production has steadily increased since mid-1980s. Triticale is currently cultivated on about 3.7 million ha in Europe in 2016, where Poland, Belarus, Germany, and France, are the main producers with 89% of the total European triticale acreage (FAOSTAT 2018). With the increasing acreage FHB has become an important issue for farmers especially for pig and poultry producers due to the risk for livestock of being fed with contaminated triticale grain (Góral et al., 2002; Murugesan et al., 2015; Pierron et al., 2016).

Genetic bridging (traits and markers) between triticale and wheat

The genetic proximity between triticale and wheat simplify the transfer of technologies and the use of genetic knowledge. As a major crop for human feed, wheat benefits indeed of massive investments for research and represents a valuable reservoir of information (Shiferaw et al., 2013).

Diversity inputs from Wheat and relatives

Results of interspecific hybridization between wheat and triticale has been extensively study in the past (Hao et al., 2013; Jenkins, 1969; Kiss, 1966; Lukaszewski & Gustafson, 1983; Merker, 1975; Sanchez-Monge, 1958). This hybridizations has been used to improve the resistance and the agronomic features of both crops, triticale and wheat (Hills et al., 2007; Kang et al., 2016; Lukaszewski & Gustafson, 1983; Nkongolo et al., 1991; Oettler et al., 2005; Saulescu et al., 2011). Triticale breeding benefits from the large genetic variation present in the original species, wheat and rye, and from their relatives. As an example, Kwiatek et al. (2016) developed an hexaploid triticale carrying leaf rust resistance gene *Lr32* via crossing triticale with an Aegilops tauschii–rye amphiploidy and Kang et al. (2016) developed hexaploidy triticales showing high level of stripe rust resistance by generating trigeneric hybrids, crossing wheat, rye and *Psathyrostachys huashanica*.

Technology Transfer

Simple sequence repeat (SSR) markers, also called microsatellites, have been commonly used over the past years (Vieira et al., 2016). They are highly polymorphic, co-dominant, and high density SSR maps are available for wheat (Somers et al., 2004), for rye (Hackauf et al., 2003, Khlestkina et al., 2004; Korzun et al., 2001) and for triticale (Balážová et al., 2014; Tyrka et al., 2011; Vyhnánek et al., 2009). The transferability rates of SSR markers from wheat and rye to triticale have been estimated at 58% and 39% respectively (Kuleung et al., 2004).

Single nucleotide polymorphism (SNP) are today used in preference in genomic studies, QTL mapping and marker assisted selection (MAS) (Jehan & Lakhanpaul, 2006; Semagn et al., 2006; Semagn et al., 2014). They are co-dominant, much more abundant than SSR markers and easily amenable to automation (Jehan & Lakhanpaul, 2006; Semagn et al., 2006). Although the transferability of rye and wheat SNP to triticale is feasible (Haseneyer et al., 2011; Leach & Dundas, 2006), there is no SNP chip-based technology currently available for triticale. A high-density map for a DH triticale population has however been generated in 2018 by Dhariwal et al. (2018) using a wheat 90K Infinium iSelect SNP assay and a rye 10K SNP assay provided by KWS LOCHOW GMBH, Bergen, Germany. Despite efficient, this system of double genotyping based on the use of two assays is particularly costly.

Genotyping by sequencing (GBS) is an emerging method which has greatly increased the number of SNP available (Elshire et al., 2011; He et al., 2014). The transfer of this technology for wheat genotyping has required the elaboration of a specific protocol with two enzymes for DNA reduction instead of one (Poland et al., 2012). The DArTseq technology, developed by the DArT company, is a variant of the GBS technique. It generates a large amount of SNP and presence absence variation (PAV) in a throughput and cost effective way (Cruz et al., 2013). Available for triticale, the technique has been elaborated using the same enzymes couple than the one developed for wheat. A genetic map integrating microsatellite, DArT array and DArTseq markers is available for triticale (Tyrka et al., 2015).

Fusarium head blight in small grain cereals: a threat to yield, quality and health

Economic importance

Fusarium Head Blight (FHB), caused mainly by *Fusarium graminearum* and *Fusarium culmorum*, is considered a disease of major importance in most areas of the world where wheat and other small grain cereals are grown (Bai & Shaner, 1994, 2004; Mesterházy et al., 2005; Ruckenbauer et al., 2001; Schroeder & Christensen, 1963). Fusarium species are non-host specific and can infect all members of the *Gramineae* in temperate and semi-tropical areas (Arseniuk et al., 1999; Mcmullen et al., 1997; Van Eeuwijk et al., 1995). They may significantly damage cereal crop within a few weeks after flowering (Mcmullen et al., 1997; Parry et al., 1995; Windels, 2000). Yields can be dramatically reduced. Quality is affected due to the destruction of starch granules and storage protein (Dexter et al., 1996, Nightingale et al., 1999). Finally, the contamination of the harvest by secondary fungal metabolites, known as mycotoxins, can devalue or even render the crop unsuitable for food and feed uses (D'Mello et al., 1999; Desjardins, 2006; Kotowicz et al. 2014; Mesterházy et al., 1999; Windels, 2000). Mycotoxin contaminations in cereals for downstream processing, such as milling, production of bio-ethanol or brewing, are even more crucial since toxins tend to concentrate in the by-products, such as bran and Distiller's Dried Grains with Solubles (DDGS) that are commonly used as animal feed (Pinotti et al., 2016; Schedle et al. 2010; Schaafsma et al. 2009). FHB as emerged as a disease of economic importance since the 1990's (Windels, 2000). The importance of the damages strongly depends of the weather. The development of the disease is faster in warm and humid conditions (Rossi et al., 2001), especially when these conditions appear around anthesis when cereals are most susceptible (Osborne & Stein, 2007). Several studies conclude on a rise of the strength and the frequency of the attacks in the future due to climatic changes (Del Ponte et al., 2004; Melloy et al., 2010). The importance of the damages already generated by FHB and the probable increase of the attacks frequency make this plant disease one of the most concerning in the world.

Causal organisms and geographical repartition

Fusarium head blight has been associated with up than 17 causal organisms (Saharan et al., 2004). The most common species associated with FHB are *Fusarium graminearum* (*Gibberella zeae*), *F. culmorum*, *F. avenaceum* (*G, avenacea*), *F. poae* and *Microdochium nivale* (*Monographella nivalis*). *F. graminearum* and *F. culmorum* show the highest level of pathogenicity (Fernandez & Chen, 2005). Several organisms use to coexist within the same field or even within the same plant (Siou et al., 2015; Xu et al., 2005). Abundance of the different causal agents depends on geographical location and climatic conditions, particularly temperature and moisture (Xu et al., 2007, 2005). *F. graminearum* predominates largely under warm and wet conditions and is considered the most prevalent species in USA, Canada, Australia and central Europe. In the cooler maritime regions, as northwest Europe, *F.culmorum* predominates, and *F. poae* and *Microdochium nivale* have a greater importance. A shift to a prevalence of F. graminearum has however been observed in these regions during the last decade (Jennings et al., 2004; Waalwijk et al., 2003). To finish, *F. avenaceum* is present in all these areas but always in small proportion (Parry et al., 1995; N. S. Wegulo, 2012).

Systematics of Fusarium species

Kingdom: Fungi

Division: Ascomycota

Subdivision: Pezizomycotina

Class: Sordariomycetes

Order: Hypocreales

Family: Hypocreaceae

Genera: Gibberella or Nectria

Figure 1: Systematic of Fusarium species

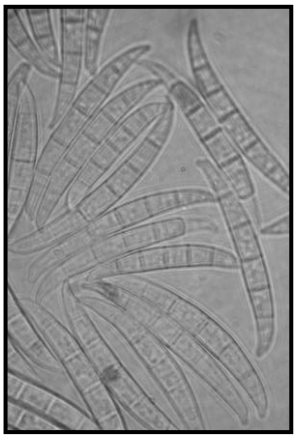

Figure 2: Conidia *(F. graminearum)**

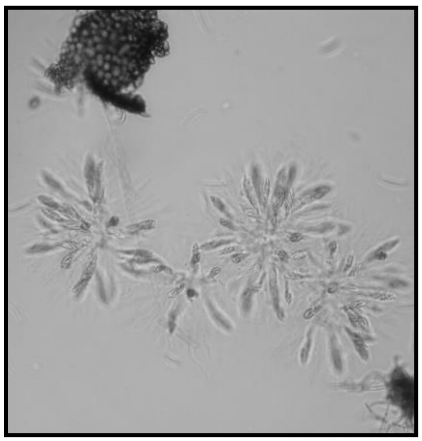

Figure 3: Ascospores & Perithecium (*F. graminearum)**

*Pictures kindly provided by Pr. Marc Lemmens

The disease was first described by W. G Smith in 1884 under the name “wheat scab” and was renamed “Fusarium head blight” by Atanasoff in 1920. In 1935, Wollenweber & Reinking revolutionize *Fusarium* systematic by describing *Fusarium* species as mitosporic Ascomycetes and by grouping species into 16 sections. Later in 1996, O’Donnell (1996), offer more precisions in *Fusarium* species classification thanks to molecular phylogenetics methods.

Life cycle

FHB pathogens are non-host specific organisms and can survive on many plants, including cereals such as bread and durum wheat, barley, oat, maize, rye or triticale (Becher et al., 2013; Parry et al., 1995). Several species of Fusarium, including, *F. graminearum* may also live asymptomatic on grass hosts (Inch and Gilbert 2003) and can survive saprotrophically in the soil more than 4 years (Leplat et al., 2013).

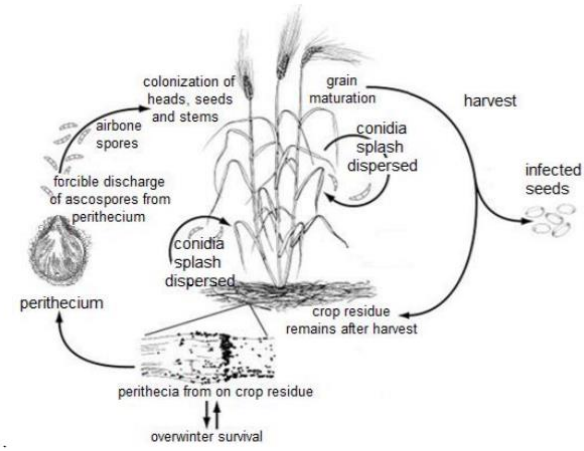

Figure 4: The life cycle of *Fusarium graminearum* [teleomorph: *Gibberella zeae*] causing Fusarium head blight on wheat under field condition (Trail, 2009)

Initial source of inoculum for FHB epidemics comes from colonized plant residues (Becher et al., 2013). The conidia and ascospores present on these residues reach the cereal spikelets thanks to wind and rain splash (Osborne & Stein, 2007). After germination, the fungal hyphae colonize the floral cavity and penetrate into the plant via susceptible floret tissues such as anthers or natural opening such as stomata (Bushnell et al., 2003; Walter et al., 2010).

After a brief biotrophic period, the pathogen shifts to a necrotrophic phase leading to the host cell death (Brown et al., 2010; Kazan et al., 2012). While colonizing the cells, the fungus synthesizes trichothecene mycotoxins, notably deoxynivalenol (DON), which enables the spreading of the fungus through the rachis and the colonization of adjacent florets (Bai et al., 2002).

Symptoms

Figure 5: Triticale head showing Fusarium head blight symptoms with premature bleached spikelets

Initial infection starts with small and brown water-soaked lesions on the glume, or on the rachis. It then spreads in all directions from the point of infection. A salmon-pink fungal growth may be seen along the edge of the glumes or at the base of the spikelet (Saharan, 2004). Penetration of the fungus in the rachis leads to vascular dysfunction associated with premature ripening of the spike above the point of infection, also termed as wilting (Goswami & Kistler, 2004).

Figure 6: Triticale kernels with Fusarium symptoms

Diseased kernels tend to appear smaller, shriveled and show white to pale pink discoloration (Abramson et al., 1987; Mesterházy et al., 2005; Ruckenbauer et al., 2001). The visual symptoms are associated with mycotoxin accumulation in the kernel (N. S. Wegulo, 2012)

Risk of mycotoxins contamination

The main concern associated with FHB contamination is the accumulation in the kernels of secondary fungal metabolites, known as mycotoxins, which can devalue or even render the crop unsuitable for food and feed uses (D'Mello et al., 1999; Desjardins, 2006; Kotowicz et al., 2014; Mesterházy et al., 1999; Windels, 2000). Among the numerous Fusarium mycotoxins, DON and its derivatives are the most prevalent ones (Joffe, 1986; Miedaner et al., 2004; Rotter, 1996). They are harmful to both humans and livestock when ingested (Ghareeb et al., 2015; Gilbert & Tekauz, 2000; Pestka, 2010). Numerous countries have established guidelines or regulations for maximum DON content in cereals and cereal products in order to ensure the safety of food and feed (Van Egmond & Jonker, 2004). As an example, the

European authorities have set a limit of 1.25 mg/kg DON in unprocessed cereals other than durum wheat, oats and maize (Commission Regulation (EC) No. 1126/2007).

Phenotyping for FHB resistance

Types of resistance

FHB resistance is a complex trait and several types of mechanism underlying the genetic resistance have been described (Mesterházy, 1989, 1995; Mesterházy et al., 1999; Miller et al., 1985; Schroeder & Christensen, 1963). Resistance to initial infection (type 1) and resistance to fungal spread from an infected floret along the rachis (type 2) were first described by Schroeder and Christensen (1963). Resistance to deoxynivalenol (DON) accumulation, also known as type 3 resistance (Miller et al., 1985) is positively correlated with the resistance to kernel infection (Buerstmayr & Lemmens, 2015; Paul et al., 2005, 2006), also termed as type 4 resistance (Mesterházy et al., 1999). Finally, tolerance to Fusarium head blight was characterized as type 5 (Mesterházy, 1989, 1995, Mesterházy et al., 1999). The thousand kernel weight (TKW) has been used as an indication of the level of tolerance to Fusarium head blight (Saur 1984, Saurand Trottet 1986). The objective was to characterize differences in yield when primary disease symptoms do not show significant differences (Caldwell, 1968, Robinson, 1969, Simons, 1969, Russel, 1978, Mackey, 1986).

Morphological traits related with FHB resistance

Aside from the above-described resistance mechanisms, plant height, ear morphology, or earliness can also significantly influence resistance to FHB (Boeven et al., 2016; Buerstmayr et al., 2012; Buerstmayr et al., 2011; Draeger et al., 2007; Kalih et al., 2014; Klahr et al., 2007; Mesterházy, 1995; Miedaner et al., 2017; Paillard et al., 2004; Schmolke et al., 2008; Steiner et al., 2019). The widely deployed Norin 10 semi-dwarfing *Rht* alleles, namely *Rht-B1b* and *Rht-D1b*, have been found associated with increased FHB susceptibility in bread wheat (Hilton et al., 1999; Mao et al., 2010; Miedaner & Voss, 2008), and in durum wheat (Buerstmayr et al., 2012; Prat et al., 2017). Similarly, the dwarfing allele of the *Ddw1* gene commonly deployed in triticale germplasm and located on the rye chromosome 5R (Korzun et al., 1996) has been found to be related with increased FHB susceptibility in triticale (Kalih et al. 2014).

Scoring strategy

The overall FHB resistance in field used to be assessed by evaluating the proportion of infected spikelets on a whole plot basis after spray inoculation (Buerstmayer et al. 2009; Parry et al. 1995). This method is considered to reflect the genotypic response during natural epidemics. It encompasses an integrated measure for FHB severity but does not distinguish types of resistance in the sense of Schroeder and Christensen (1963). The number of infected spikelets can be directly correlated with the number of damaged kernels. Some genotypes can however show invasion of seeds without visible sign of damage on hulls (Schroeder & Christensen 1963). Scoring for additional types of resistance is therefore of high interest.

The mycotoxin DON can be detected and quantified in grains by different analytical approaches, such as high-performance liquid chromatography (HPLC), gas chromatography coupled with mass spectrometry (GC-MS) (Koch, 2004; Krska et al., 2007), or enzyme-linked immunosorbent assays (ELISA) (Dos Santos et al., 2011; Maragos & McCormick, 2000; Sinha et al., 1995). Despite feasible, the measurement of toxin content is time consuming, costly and not routinely performed on high numbers of samples as typical for a breeding program. Alternative systems for assessing DON content using optical methods are available and have been reviewed by Saccon et al. (2017). Commonly used techniques include fluorescence, visible and infrared spectroscopy (Jin et al., 2014; Peiris et al., 2010), or multispectral and hyperspectral imaging (Barbedo et al., 2015). Most of these techniques require sophisticated equipment, difficult calibration steps, and significant investment, and are therefore rarely implemented in breeding programs.

Breeders favor instead visual scorings to estimate the proportion of Fusarium damaged kernels (FDK) on harvested grain samples (Abramson et al., 1987; Mesterházy et al., 2005; Ruckenbauer et al., 2001). Previous studies have frequently found significant and positive correlations between FDK and DON content (Buerstmayr & Lemmens, 2015; Paul et al., 2005, 2006). In an extensive meta-analysis, Paul et al. (2005) compared the association between different visual measures of FHB incidence and severity and concluded that FDK had the strongest average association with DON content (r=0.73). Among 100 studies used for this meta-analysis correlation coefficients (r) between FDK and DON content ranged from -0.47

to 0.98, with 80% of r>0.5 and only 2% r<0. While FDK has a strong relationship with DON content in grains this method has several drawbacks as being time and labor intensive. Moreover, FDK estimation requires skilled assessors and can be subjective and assessor-dependent.

Digital image analysis is a promising alternative to simplify FHB severity assessment on grains. It can be automatized, easily applied to many samples, offers the advantage to be fast, non-destructive, and does not suffer from assessor effects that may impede scoring accuracy. In addition, the raw and the analyzed digital images can be saved and remain easily available for follow up analyses as opposed to the conservation of the kernels themselves. Presently, there have been methods based on RGB (red, green and blue) analyses which have been developed to detect Fusarium infection (Jirsa & Polišenská, 2011; Wiwart et al., 2011) or to approximate Fusarium damaged kernels (Maloney et al., 2014). These are cost-effective, require only basic technical infrastructure and data processing is straight forward.

Genetic resistance for Fusarium head blight

Genetic resistance: a key solution in fusarium head blight management

Strategy of Fusarium head blight management aimed at reducing the amount of primary inoculum, hampering the inoculum dispersal and limiting the infection when inoculum is present (Parry et al. 1995). Adapted cultural practices, notably crop rotation and tillage, enable a significant reduction of the amount of inoculum (Dill-Macky & Jones, 2000). Chemical control measures are only partly effective in controlling Fusarium in small grain cereals and complex to set on regarding the narrowness of the application window (Mankeviciene et al., 2008; Šíp et al., 2010; Stack, 2000). Host resistance is particularly interesting for Fusarium management as the genetic resistance to FHB in small grains is non-race specific, quantitatively inherited and has a moderate to high heritability (G. Bai & Shaner, 1994; Van Eeuwijk et al., 1995). The use of FHB-resistant cultivars combined with appropriate crop management practices is considered the most efficient method for managing this disease (Blandino et al. 2013; Buerstmayr et al., 2009; McMullen et al. 2008; Parry et al., 1995; Wegulo et al., 2010). Therefore, breeding cereal cultivars which are resistant to Fusarium head blight and to the associated mycotoxin contaminations plays a crucial role for an integrated and sustainable management of this disease.

Genetic architecture of FHB resistance in triticale

The resistance of modern triticale varieties against FHB ranges approximately between its parents wheat and rye (Kiecana et al., 1987; Langevin et al., 2004; Miedaner et al., 2001) allowing genetic improvement via resistance breeding by recurrent selection and molecular breeding (Miedaner et al., 2004; Oettler & Wahle, 2001). Several recent studies have been conducted to understand FHB resistance in triticale and to elucidate its genetic architecture. Four doubled-haploid triticale populations were evaluated for resistance to FHB by Kalih et al. (2015) and 17 quantitative trait loci were identified on chromosome 2B, 3B, 4B, 4R, 5A, 5B, 5R, 6A, 6B, 7R. Miedaner et al. (2016) evaluated resistance on multiple FHB-related traits in a doubled haploid winter triticale population. A common quantitative trait locus for all FHB-related traits was found on wheat chromosome 2A being of minor importance for FHB severity, but of high importance

for DON content and FDK rating. Another QTL on rye chromosome 5R was more important for FHB severity. 17 major quantitative trait loci for multiple FHB-related traits have been identified by Dhariwal et al. (2018) on chromosomes 1A, 2B, 3A, 4A, 4R, 5A, 5R and 6B in a doubled haploid spring triticale population. Finally, Galiano-Carneiro et al. (2018) performed the first genome-wide association study for FHB resistance in triticale. QTL for FHB resistance were identified on chromosomes 2A, 2B, 5B and 3R. Collectively these findings highlight the potential of genomics-assisted approaches to improve Fusarium resistance in triticale.

This relatively reduced number of studies provides to breeders a limited description of the genetic architecture of FHB resistance in triticale, while numerous studies have been published on molecular mapping of FHB resistance in wheat. 52 quantitative trait loci (QTL) mapping studies, nine research articles on marker-assisted selection and seven on marker-assisted germplasm evaluation were summarized by Buerstmayr et al. (2009). In total, more than 100 QTL for FHB resistance were detected on all wheat chromosomes except chromosome 7D, and 22 were found in several independent mapping studies. A QTL meta-analysis approach combining QTL of 30 mapping populations was conducted by Löffler et al. (2009) and 19 MQTL were found on 12 chromosomes. While Liu et al. (2009) clustered 119 significant QTL for FHB resistance on 21 chromosomes, based on 45 studies. Since most of the identified QTL are located on the A and B genomes, bread wheat represents a promising reservoir and resource of resistance for triticale.

Among the QTL for FHB resistance identified in bread wheat, those on chromosomes 3BS (*Fhb1*) and 5AS (*Qfhs.ifa-5A*) are the most prominent ones (Buerstmayr et al. 2009). Both derive from the well-known resistance donor Sumai-3 (Buerstmayr et al., 1999; Waldron et al., 1999). *Fhb1* is a well-characterized QTL which has been validated in numerous studies and confers a high level of FHB resistance to fungal spreading (type 2 resistance) (Agostinelli et al., 2012; Anderson et al., 2001; Balut et al., 2013; Bourdoncle & Ohm, 2003; Buerstmayr et al., 2002, 2003; Chen et al., 2006; Jiang et al., 2007; Mccartney et al., 2007; Prat et al., 2017; Shen et al., 2003; Waldron et al., 1999). *Qfhs.ifa-5A*, on the other

hand, has been shown mainly to increase resistance to initial infection (type 1) (Buerstmayr et al., 2003; Lin et al., 2006; Xue et al., 2011) and is tightly associated with high anther extrusion in bread wheat (Steiner et al., 2019).

Introgression of *Fhb1* and *Qfhs.ifa-5A* into European winter wheat lines did not lead systematically to a negative drag regarding yield and quality but was highly efficient for increasing FHB resistance (Salameh et al., 2011; von der Ohe et al., 2010). As an example, the variety Jaceo, registered in France in 2012 (Syngenta Seeds), was the first variety carrying *Fhb1* commercially available in Europe.

Objectives of the thesis

Breeding and growing varieties that resist mycotoxin accumulation are of foremost importance for crops such as triticale, which are used primarily on the farm as animal feed, without checking for a potential mycotoxin contamination of the harvest. To date, FHB resistance from bread wheat has never been exploited to improve the resistance of triticale. Three related mapping populations with bread wheat introgressions were generated for this PhD. The impact of the two major bread wheat QTL for FHB resistance, *Fhb1* and *Qfhs.ifa-5A*, was evaluated in three elite triticale backgrounds. These mapping populations were phenotyped for Fusarium head blight resistance in replicated field trials under artificial inoculation. This work constitutes the first characterization of FHB resistance derived from bread wheat into elite triticale backgrounds.

The aims of this PhD were: (i) to quantify and validate the effect of *Fhb1* and *Qfhs.ifa-5A* in triticale genetic background (ii) getting further insight into the genetic architecture of FHB resistance in triticale beyond these two major effect QTL, (iii) investigate the association of plant height and FHB resistance with specific focus on the semi-dwarfing gene *Ddw1*, and iv) improve the scoring quality for FHB severity by developing a new scoring method automated and adapted for breeding.

Publication 1: Whitened kernel surface: A fast and reliable method for assessing Fusarium severity on cereal grains by digital picture analysis

Publication 2: QTL mapping and successful introgression of the spring wheat derived QTL *Fhb1* for Fusarium head blight resistance in three European triticale populations

PUBLICATION 1

TITLE

Whitened Kernel Surface: A fast and reliable method for assessing Fusarium severity on cereal grains by digital picture analysis

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ORIGINAL ARTICLE

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Whitened kernel surface: A fast and reliable method for assessing Fusarium severity on cereal grains by digital picture analysis

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Abstract

Fusarium head blight (FHB) is a cereal disease of major importance responsible for yield losses and mycotoxin contaminations in grains. Here, we introduce a new measurement approach to quantify FHB severity on grains based on the evaluation of the whitened kernel surface (WKS) using digital image analysis. The applicability of WKS was assessed on two bread wheat and one triticale grain sample sets (265 samples). Pearson correlation coefficients between Fusarium-damaged kernels (FDK) and WKS range from $r = 0.77$ to $r = 0.81$ and from $r = 0.61$ to $r = 0.86$ for the correlation between deoxynivalenol (DON) content and WKS. This new scoring method facilitates fast and reliable assessment of the resistance to kernel infection and shows significant correlation with mycotoxin content. WKS can be automated and does not suffer from the "human factor" inherent to visual scorings. As a low-cost and fast approach, this method appears particularly attractive for breeding and genetic analysis of FHB resistance where typically large numbers of experimental lines need to be evaluated, and for which WKS is suggested as an alternative to visual FDK scorings.

KEYWORDS
digital picture analysis, DON, FDK, Fusarium head blight, resistance, WKS

1 | INTRODUCTION

Fusarium head blight (FHB) is considered a disease of major importance in most areas of the world where wheat and other small grain cereals are grown. FHB can infect all members of the *Gramineae* and

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may significantly damage a crop within a few weeks (McMullen, Jones, & Gallenberg, 1997; Parry, Jenkinson, & McLeod, 1995; Windels, 2000). In addition to yield losses, the contamination of the harvest with secondary fungal metabolites, known as mycotoxins, may devalue or even render the crop unsuitable for consumption (Desjardins, 2006; D'Mello, Placinta, & Macdonald, 1999; Kotowicz, Frąc, & Lipiec, 2014; Mesterhazy, Bartok, Mirocha, & Komoroczy, 1999; Windels, 2000). Among these mycotoxins, deoxynivalenol (DON) and its derivatives are the most prevalent ones (Joffe, 1986; Rotter, Prelusky, & Pestka, 1996) and are harmful to both humans and livestock when ingested (Gilbert & Tekauz, 2000; Sobrova et al., 2010). Numerous countries have established guidelines or regulations for maximum DON content in cereals and cereal products in order to ensure food and feed safety (Van Egmond & Jonker, 2004). European authorities have fixed a limit of 0.75 mg/kg DON in cereals intended for direct human consumption (Commission Regulation (EC) No.), while in the United States, the recommended threshold has been set at 1 mg/kg (Guidance for Industry & FDA,).

Cultivation of Fusarium-resistant cultivars plays a pivotal role in Fusarium control and for the prevention of mycotoxin contamination. Breeding for resistance to mycotoxin accumulation is therefore a top priority and receives high attention in research and cultivar development (Buerstmayr & Lemmens, 2015). Some of the approaches and methods used for FHB resistance breeding have been reviewed by Buerstmayr, Ban, and Anderson (2009). Identification of resistant breeding lines relies on the availability of tools and methods for measuring the trait of interest in a reproducible and cost-effective manner. The mycotoxin DON can be detected and quantified in grains by different analytical approaches, such as high-performance liquid chromatography (HPLC), gas chromatography coupled with mass spectrometry (GC-MS) (Koch, 2004; Krska, Welzig, & Boudra, 2007) or enzyme-linked immunosorbent assays (ELISA) (Dos Santos et al., 2011; Maragos & McCormick, 2000; Sinha, Savard, & Lau, 1995). Despite feasible, the measurement of toxin content is time-consuming, costly and not routinely performed on high numbers of samples as typical for a breeding programme. Alternative systems for assessing DON content using optical methods are available and have been reviewed by Saccon, Parcey, Paliwal, and Sherif (2017). Commonly used techniques include fluorescence, visible and infrared spectroscopy (Jin et al., 2014; Peiris et al., 2010), or multispectral and hyperspectral imaging (Barbedo, Tibola, & Fernandes, 2015). Most of these techniques require sophisticated equipment, difficult calibration steps and significant investment and are therefore rarely implemented in breeding programmes.

In order to assess FHB symptom severity, breeders often rely on visual scoring on the plants and/or estimate visually the proportion of Fusarium-damaged kernels (FDK) on harvested grain samples. Diseased kernels tend to appear smaller, shrivelled and show white to pale pink discoloration (Abramson, Clear, & Nowicki, 1987; Mesterházy et al., 2005; Ruckenbauer, Buerstmayr, & Lemmens, 2001). Previous studies have frequently found significant and positive correlations between FDK and DON content (Buerstmayr & Lemmens, 2015; Lemmens et al., 2016; Paul, Lipps, & Madden, 2005, 2006). In an extensive meta-analysis, Paul, Lipps, and Madden (2005) compared the association between different visual measures of FHB incidence and severity and concluded that FDK had the strongest average association with DON content (r = 0.73). Among 100 studies used for this meta-analysis correlation coefficients (r) between FDK and DON content ranged from −0.47 to 0.98, with 80% of $r > 0.5$ and only 2% $r < 0$. While FDK has a strong relationship with DON content in grains, this method has several drawbacks as being time- and labour-intensive. Moreover, FDK estimation requires skilled assessors and can be subjective and assessor-dependent.

Digital image analysis is a promising alternative to simplify FHB severity assessment on grains. It can be automatized, easily applied to many samples, offers the advantage to be fast, non-destructive and does not suffer from assessor effects that may impede scoring accuracy. In addition, the raw and the analysed digital images can be saved and remain easily available for follow-up analyses as opposed to the conservation of the kernels themselves. Presently, there have been methods based on RGB (red, green and blue) analyses which have been developed to detect Fusarium infection (Jirsa & Polišenská, 2011; Wiwart, Koczowska, & Borusiewicz, 2001) or to approximate Fusarium-damaged kernels (Maloney et al., 2014). These are cost-effective and require only basic technical infrastructure, and data processing is straightforward.

Here, we describe a new approach to quantify FHB severity on grains which employs digital image analysis for an automated estimation of the whitened kernel surface (WKS). The main objectives of this study were (a) developing a protocol for WKS measurement and (b) evaluating whether WKS measurement is a competitive and robust method for measuring Fusarium-induced damages on grain samples in breeding and/or research programmes.

2 | MATERIALS AND METHODS

2.1 | Plant material

Two sets of bread wheat (*Triticum aestivum* L.) and one set of triticale (*Triticosecale* Wittm.) grain samples were analysed in this study. The first set of bread wheat samples (BW1) comprised 98 breeding lines from the winter wheat breeding programme of the Austrian company Saatzucht Donau. The second bread wheat set (BW2) consisted of 78 varieties and breeding lines from the winter wheat breeding programme of the French company Florimond-Desprez. The triticale samples (TRIT) were 37 experimental lines descending from a cross between the FHB-resistant triticale line G8.06 with the susceptible cultivar 'Tulus'. The FHB-resistant breeding line G8.06 possesses the *Fhb1* allele from the FHB-resistant wheat cultivar 'Sumai-3', and 'Tulus' is a registered variety bred by Nordsaat Saatzucht GmbH, Germany.

2.2 | Acquisition of Fusarium-infected grain samples

The triticale lines and the bread wheat lines from Saatzucht Donau were evaluated in Fusarium-inoculated field experiments to generate

two sets of infected grain samples, TRIT and BW1, respectively. Field experiments were carried out at IFA-Tulln, Austria (48.3185°N 16.0690°E, 177 m above sea level), in 2014 for TRIT and in 2015 for BW1. Experimental layout and the applied Fusarium inoculation method were similar to Buerstmayr and Buerstmayr (2016). Briefly, experimental plots consisted of 0.5-m^2 double row plots of 1 m length. At anthesis, heads were spray-inoculated with the DON producing *F. culmorum* isolate Fc91015 at 1.25×10^6 conidia/m^2 for BW1 and the isolate IFA104 at 2.5×10^6 conidia/m^2 for TRIT. Inoculum suspensions were prepared as described in Buerstmayr, Steiner, Lemmens, and Ruckenbauer (2000). The crop canopy was kept moist by mist irrigating during 20 hr after inoculations to facilitate spore germination and infection.

Bread wheat genotypes from Florimond-Desprez (BW2) were tested in experimental fields in France. Plots were 1.13-m^2 large triple rows of 1.5 m length. One field trial was conducted with all the 78 varieties in 2015 at Cappelle-en-Pévèle (50.5156°N 3.1651°E, 40 m above sea level). At anthesis, heads were spray-inoculated with the DON producing *F. graminearum* isolate Fu1008 at a rate of 11.1×10^6 conidia/m^2. In addition, a subset of 13 varieties was evaluated in 2015 at 4 locations in France (Cappelle-en-Pévèle: 50.5156°N 3.1651°E, 40 m above sea level; Froissy: 49.5650°N 2.2280°E, 175 m above sea level; Prémesques: 50.6713°N 2.9519°E, 42 m above sea level; and Rennes: 48.1437°N 1.7048°W, 75 m above sea level), resulting in 65 additional grain samples. Soil surface inoculation was done by spreading naturally FHB-infected cornstalks (one per square metre) in the experimental fields.

For all kernel sets, field plots were harvested at full ripening using a plot combine harvester set to low wind speed in order to avoid the loss of light-weight Fusarium-infected kernels.

2.3 | Evaluation and measurement of the resistance to Fusarium

Three subsamples of grains of 20 grams each were collected from each harvested sample of BW1 and BW2. The first subsample was used to measure the DON content, the second to visually score FDK and the third to assess WKS. Two subsamples of grains of 20 grams each were taken from each of the triticale lines (TRIT). The first subsample was used to measure the DON content, the second for both FDK and WKS assessment. All those subsamples were taken from the combine-harvested bulk sample using a grain divider to obtain representative and unbiased subsamples.

In order to evaluate the proportion of Fusarium-damaged kernels (FDK), grain samples were inspected in blue seed trays (8×14 cm) by three assessors, one assessor per sample set. Visual evaluations of FDK were determined by comparing to exactly counted control samples with 1%, 5%, 20%, 50%, 75%, 95% and 100% FDK. The criteria to visually identify Fusarium-damaged kernels were grain size, colour and shrivelling.

Direct competitive enzyme-linked immunosorbent assay (ELISA) kits were used to determine the DON concentration in the grain samples. The test AgraQuant® ELISA DON (Romer Labs Diagnostic GmbH, Tulln, Austria) was used for BW1, and the test Ridascreen® Fast DON (R-Biopharm AG, Darmstadt, Germany) was used for BW2, and TRIT. DON extraction, calibration and reading were performed according to the manufacturers' instructions.

Digital evaluation of the whitened kernel surface (WKS) has been established and used as new approach to quantify visible Fusarium damages on grain samples. To generate a digital image, 20 grams of grain from each seed sample was poured in bulk on a blue-tinted paper sheet (Clairefontaine Trophée, intensive blue, A4, 160 g/m^2, Exacompta Clairefontaine SA, France) and spread swiftly on the paper to minimize overlapping of grains. Samples were photographed using a digital camera (PowerShot G10, Canon Inc., Japan), which was fixed on a tripod, 40 cm above the kernels. The camera was set to ISO 200, focal length 28 mm, aperture F/5.0, shutter speed 1/50, with a resolution of 11 megapixels (4416×2480), and photographs were triggered with a remote shutter release to avoid camera movement and obtain sharp images. At the beginning of each photograph session, the white balance was manually set according to manufacturer instructions by using a neutral grey card (JJC GC-1, Shenzhen JinJiaCheng Photography Equipment Co. Ltd., China). Considering the impact of light conditions on the RGB parameters of a picture, light conditions were standardized by keeping the same setup of the photo studio for all photographs. Images were taken in a dark room, and samples were illuminated with two spiral fluorescent lamps (FotoQuantum, 25 W, 5,400 K, 220–240 V, 50 Hz, Fotoquantum.com—Intelince SL, Spain) fixed above the samples diagonally opposite. After each photograph session, pictures were cropped around the portion of the image showing the kernels. The cropping process reduced the number of pixels to be examined and decreased computational time. Pictures were analysed with an own script written in Python (Python Software Foundation, Inc. Python Language Reference, version 3.4.1. available at http://www.python.org). The function "getpixel" from the Pillow library (Python Imaging Library Fork, version 2.5.3., available at https://pillow.readthedocs.io/en/latest/index.html) was used to acquire the red, green and blue-levels of each pixel (RGB levels) within a picture. These levels display values in the range of 0 to 255, which allow calculating the pixel hue (Table 1). To evaluate the whitened kernel surface, the pixels in each picture were segregated into three categories based on the RGB analysis: background pixels, healthy grain pixels and whitened grain pixels. WKS was then calculated as the percentage of whitened grain pixels among all grain pixels. One picture showing the photo studio and ten images showing samples from the set BW1, illustrating variability in Fusarium-damaged and Fusarium-whitened kernels with their respective WKS, FDK and DON content values, are available as supporting information, Figures S1 and S2, respectively.

2.4 | RGB analysis and pixel sorting

Digital picture analysis showed that the hue exhibited a bimodal distribution for all photographs (Figure 1). The first peak with an average hue around 30 was composed of pixels with a major red component. The second peak presented an average hue around 200

TABLE 1 Presentation of the Hue with Preucil's circle of colours (Preucil, 1953)

Ordering	Hue value	Hue region	Formula
R ≥ G ≥ B	0–60	Red-Yellow[a]	$x = 60^{o}\,\frac{G-B}{R-B}$ ~
G ≥ R ≥ B	60–120	Yellow-Green[a]	$x = 60^{\circ}(2 - {}^{\sim}\frac{R-B}{G-B})$
G ≥ B ≥ R	120–180	Green-Cyan[b]	$x = 60^{\circ}(2 + {}^{\sim}\frac{B-R}{G-R})$
B ≥ G ≥ R	180–240	Cyan-Blue[b]	$x = 60^{\circ}(4 - \frac{G-R}{B-R})$
B ≥ R ≥ G	240–300	Blue-Magenta	$x = 60^{\circ}(4 + \frac{R-G}{B-G})$
R ≥ B ≥ G	300–360	Magenta-Red	$x = 60^{\circ}(6 + \frac{B-G}{R-G})$

[a]Hue observable for grain pixels.
[b]Hue observable for background pixels.

and was composed of pixels with a major blue component. During the pixel sorting process, pixels of the first peak were counted as grain pixels and others were classified as background pixels. The pixels showing a major red compound with a red level lower than 75 were also counted as background pixels, as they were considered too dark to be part of a cereal grain.

Among grain pixels, distinction between healthy and whitened ones was based on their respective level of blue. A healthy grain pixel possesses a high red level, an intermediate green level and a low blue-level. In a whitened grain pixel, all three values are higher (Figure 2). During the pixel sorting process, a blue-level-limit that separates healthy grain pixels from whitened ones was determined in calibration experiments, as outlined in the following section. Pixels above this blue-level-limit were counted as whitened, and pixels bellow as healthy. To avoid classifying broken grain surfaces as Fusarium-damaged area, a maximum blue-level of 190 was set. Above this limit, pixels were considered too bright to be due to Fusarium damage and were therefore excluded from the WKS analysis. In samples without broken grains, this step is not necessary. Decision steps are summarized in Figure 3 and an example of an original and a digitally processed image of the same sample is illustrated in Figure 4.

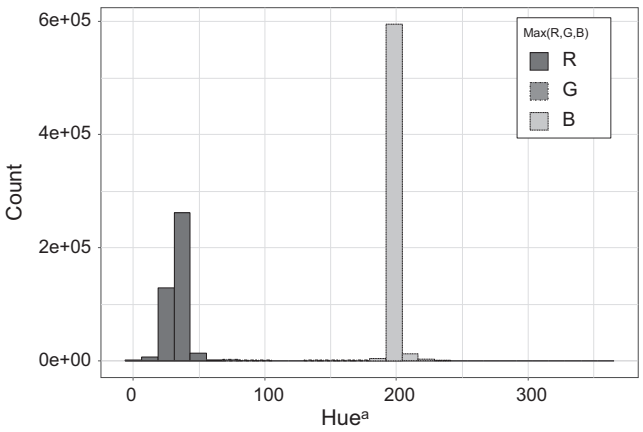

FIGURE 1 Example of the pixel hue distribution of a sample from BW1 (cf Figure 4), moderately infected, with a WKS of 7%, calculated for a blue-level-limit of 140, a FDK of 20% and a DON content of 15 ppm. [a]The Hue is a global characterization of the pixel colour, calculated based on its level of red, green and blue (cf Table 1)

2.5 | Calibration of the pixel sorting process required for WKS evaluation

The objective of the calibration process was to determine a blue-level-limit that enables an optimal discrimination of each grain pixel as either healthy or as fusarium damaged. WKS values were calculated for each grain sample for all blue-level-limits in the range of 95 to 189. Thus obtained, WKS values were correlated with the FDK and DON values in the three sample sets independently. The blue-level-limit which received the highest Pearson correlation coefficient was considered optimal for WKS estimation.

2.6 | Determination of the minimum sample size for calibration

Identifying optimal blue-level-limit for pixel sorting in new sample sets may require re-calibration. In order to assess how many samples with scored FDK and/or measured DON content are necessary for optimal pixel sorting, a cross-validation strategy was employed based on the samples of BW1. The 98 samples of BW1 were split randomly into two subsets of 49 samples each. The first subset was used for calibration and the second one for validation. Calibration sets comprising from five to forty-seven samples were picked at random in the calibration subset 1,000 times to generate 43,000 calibration runs. The impact which the number of samples in the calibration sets had on the quality of the pixel sorting process was assessed by inspecting the Pearson correlation coefficients between WKS-FDK and WKS-DON in the validation sets.

2.7 | Evaluation of the WKS repeatability

Nine bread wheat samples representing the range of visual symptom severities from low to high were chosen (samples FD1 to FD9 of BW2 cf Figure 5), and two main factors that might influence the repeatability of the WKS values were evaluated:

a Kernels overlap and orientation may modulate the WKS values. To evaluate this effect, within each of the nine bread wheat samples, kernels were mixed, poured on the blue paper sheet and photographed. This procedure was repeated 10 times for each of the nine grain samples resulting in a series of 90 pictures, 10 images per sample.

b The stability of the camera itself, due to starting and re-calibrating the white balance, may influence WKS quantification. To quantify this photograph session effect, the same nine bread wheat samples were photographed 10 times each. In this case, the camera was switched off and on again and the white balance was re-calibrated between photographs of the same sample while the grains under evaluation were not moved. This procedure also resulted in a series of 90 photographs.

2.8 | Data analysis

.Statistical analysis was performed in R 3.3.2 (R Core Team, 2016). For each trait under investigation, and each of the three grain sample sets,

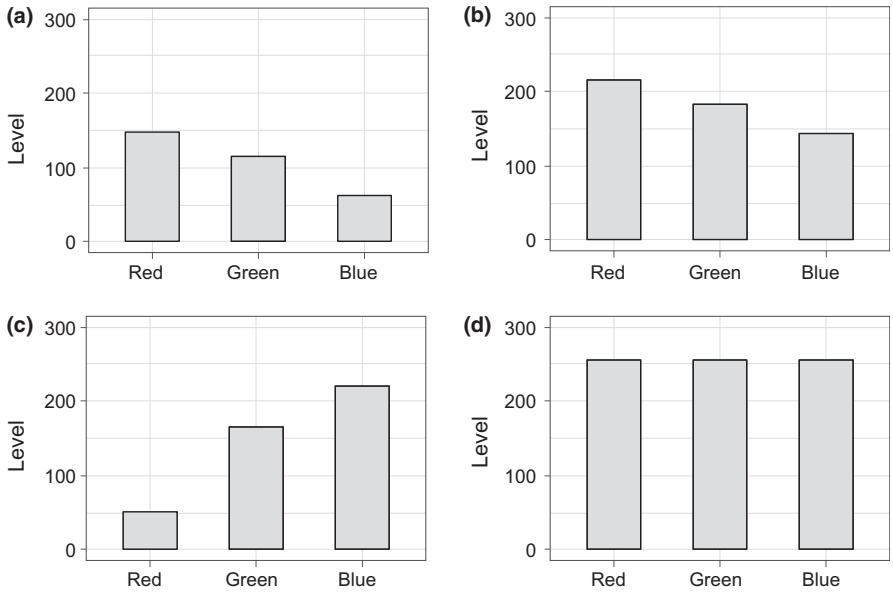

FIGURE 2 RGB features of four pixels with the pixels a, b and c coming from the picture of an infected sample of BW1 (cf Figure 4). (a) Healthy grain pixel (coordinates 222,556); (b) Fusarium-damaged grain pixel (coordinates 932,412); (c) background pixel (coordinates 200,890); (d) pure white pixel

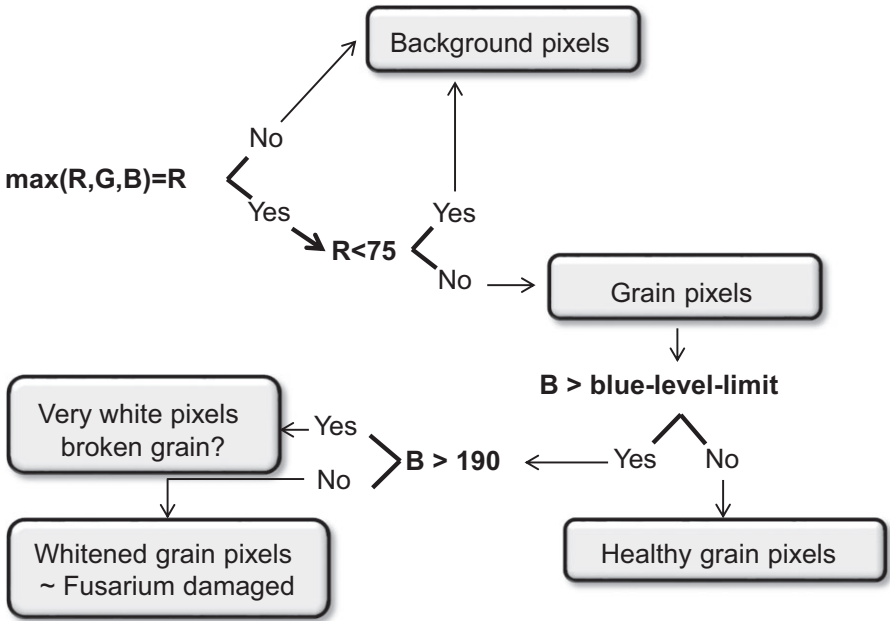

FIGURE 3 Decision tree for pixel sorting into background, healthy grains and whitened grain pixels based on their RGB features

minimum, maximum, first quartile, third quartile, mean and standard deviation were calculated. Pearson correlation coefficients for WKS-FDK, WKS-DON and FDK-DON were calculated for each kernel set. Comparisons between correlation coefficients were performed with Hotelling–Williams tests through the "multilevel" package (Bliese, 2016). Additionally, six linear regression models were fitted for each kernel set in order to relate DON to either WKS or FDK. WKS repeatability was evaluated using the "lme4" package for mixed model analysis (Bates, Maechler, Bolker, & Walker, 2015). The influence of kernels overlap and orientation on the image was examined with the 90 photographs of the first picture set (A) using the linear model:

$$\mathrm{WKS140}ij = \mu + Si + e_{ij},$$

where WKS140*ij* is the WKS value of a single image evaluated for a blue-level-limit of 140, μ the overall mean, *Si* the effect of the i^{th} sample and e_{ij} the residual variation. The same linear model was used for analysing the photograph session effect with the 90 photographs of the second picture set (B). In both linear models, the sample effects and the residuals were treated as random factors.

3 | RESULTS

3.1 | Variation in Fusarium symptom severity

Fusarium severity values within and among bread wheat kernel sets BW1 and BW2 displayed large variation from almost symptom-free and DON-free to severely diseased (e.g.,>85% FDK,>60 ppm DON). Similarly, FDK and WKS in the triticale kernel set TRIT displayed large variation (e.g.,>80% FDK), although the variation for DON content was smaller compared to the wheat samples (maximum <7 ppm DON, Figure 6 and Table 2).

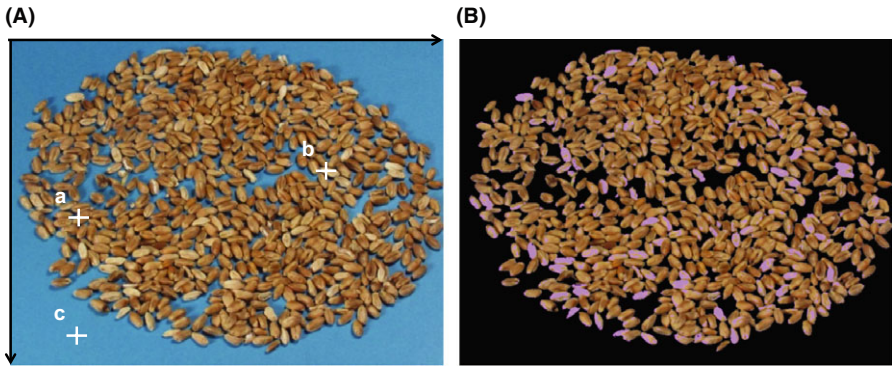

FIGURE 4 Bread wheat sample from BW1, moderately infected, with a WKS of 7%, calculated for a blue-level-limit of 140, a FDK of 20% and a DON content of 15 ppm. (A) Original picture, with 3 pixels marked. (a), healthy grain pixel (coordinates 222,556); (b), Fusarium-damaged grain pixel (coordinates 932,412); (c), background pixel (coordinates 200,890); pixels a, b and c have been described in Figure 3; (B) digitally processed picture, with background pixels artificially turned in black, and whitened grain pixels turned in pink

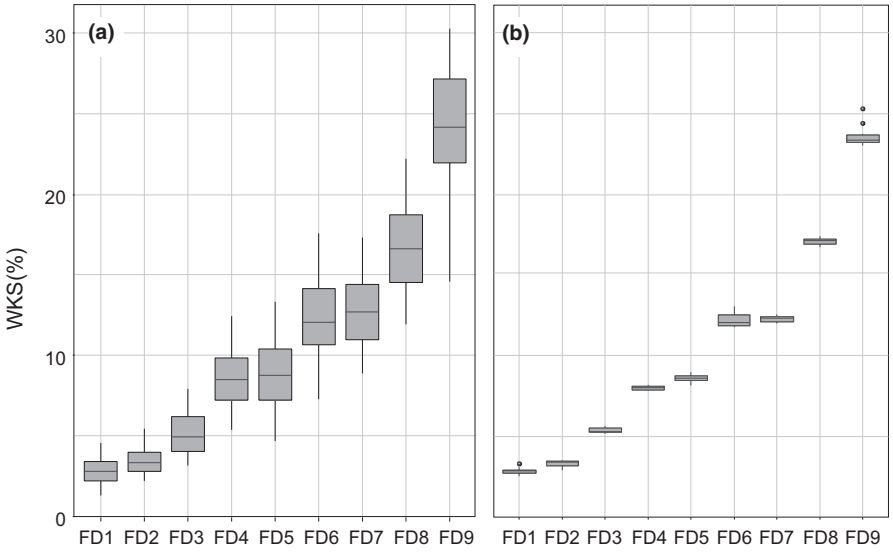

FIGURE 5 Box plots of WKS values for nine samples from the set BW2 (samples FD1 to FD9). (a) Each sample was collected mixed, poured on the blue paper and photographed ten times, while camera settings were kept constant. (b) Each sample was poured on the blue paper once and photographed ten times. For each image, the camera was re-started and re-calibrated. In both cases, WKS was calculated for a blue-level-limit of 140

3.2 | Accuracy of the calibration function of the blue-level-limit

The pixel sorting process requires an appropriate blue-level-limit to determine whether a grain pixel is counted as whitened due to Fusarium damage or not. WKS values were calculated for each grain sample for all blue-level-limits in the range of 95 to 189. Within each of the three grain sample sets (BW1, BW2 and TRIT), the Pearson correlation coefficients for WKS-FDK and WKS-DON were calculated and are presented in Figure 7. Optimal blue-level-limits and ranges of acceptable blue-level-limits were determined for each kernel set. A blue-level-limit was considered as acceptable in a relaxed sense when the value of the coefficient of correlation was less than 0.05 lower than the maximum value. The blue-level-limit was considered as acceptable in a strict sense when this reduction was less than 0.01. The optimal blue-level-limits for each of the three infected kernel sets were very similar, and the ranges of acceptable blue-level-limits were broadly overlapping among the kernel sets and for both traits, FDK and DON (Figure 7, Tables 3 and 4). WKS values obtained with a blue-level-limit between 139 and 147 yielded acceptable correlation coefficients in a strict sense with both, FDK and DON, and for each of the three kernel sets.

3.3 | Influence of the calibration set size on the accuracy of the calibration

43,000 calibration sets comprising from 5 to 47 samples were generated with samples of BW1 in order to determine the minimum number of samples required for obtaining accurate calibrations. Optimal blue-level-limits to determine WKS were calculated for each calibration set and applied to the independent validation set, to check whether they were acceptable to predict FDK and DON content in a cross-validation approach. As expected, the accuracies of the calibrations improved with increasing numbers of samples in the calibration sets (Figures 8 and 9). Two scenarios were compared (a) calibrations were calculated using FDK values (Figure 8) and (b) calibrations were based on DON values (Figure 9). A calibration set of 17 samples was sufficient to determine a blue-level-limit that

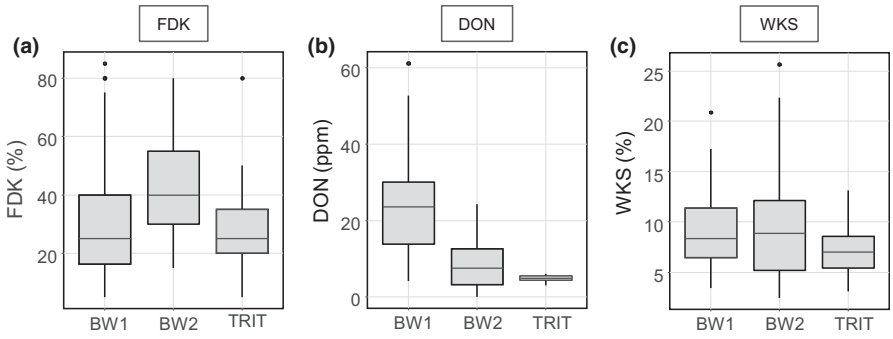

FIGURE 6 Box plots of the three infected kernel sets (BW1, BW2 and TRIT) for the three assessed traits: (a) FDK; (b) DON content; (c) WKS. The WKS has been evaluated for a blue-level-limit of 140

TABLE 2 Minimum, first quartile, mean, third quartile, maximum and standard deviation of the three populations. Student's *t* tests results, at 95% confidence limit, indicate when the mean of a population is significantly different from the mean of the two others

Trait	Set	Min	Q1	Mean	Q3	Max	Sdev	T test
DON (ppm)	BW1	4.05	14.00	23.71	30.00	61.22	11.73	***
	BW2	0.02	3.07	8.10	12.83	24.32	5.89	***
	TRIT	2.96	4.30	4.79	5.50	6.04	0.89	***
FDK (%)	BW1	5	15	31	40	85	10	*n.s*
	BW2	15	30	42	55	80	15	***
	TRIT	5	15	29	45	80	14	*n.s.*
WKS[a] (%)	BW1	3.44	6.45	9.24	11.40	20.91	3.54	*n.s.*
	BW2	2.44	5.00	9.28	12.13	25.64	4.62	*n.s.*
	TRIT	3.09	5.30	7.06	8.50	13.11	2.30	**

Note. *n.s.* non-significant.
[a]WKS evaluated with a blue-level-limit of 140.
$^{**}p < 0.01$. $^{***}p < 0.001$.

resulted in correlations between WKS-FDK and WKS-DON acceptable in a relaxed sense in more than 95% of the cross-validation scenarios. With 44 FDK measured samples in the calibration set, the correlations between for WKS-FDK and WKS-DON were acceptable in a strict sense in more than 95% of the cases (Figure 8). When calibrations were based on DON values, a calibration set size of 24 samples yielded correlations of WKS-DON and WKS-FDK acceptable in a relaxed sense in more than 95% of the cases and 47 DON measured samples led to correlations acceptable in a strict sense in more than 95% of the cross-validation scenarios (Figure 9). Thus, calibrations for finding an optimal blue-level-limit for WKS estimation are achievable with a moderate number of around 20 samples for which FDK data have been determined and do not necessarily require DON data.

3.4 | Repeatability of the WKS measure

Variability in WKS values due to the assortment of the grains on the image (A) and to the camera (B) for nine samples of wheat is shown in Figure 5. Samples with low average WKS showed smaller within-sample variation than samples with high average WKS. As an example, the variability in WKS values due to the assortment of the grains on the image was 6 times higher for sample FD9 than for sample FD1. Overall the within-sample variation due to the assortment of the grains or to the camera remained low compared to the between sample variation, resulting in high repeatability of WKS. In the first test (A), the variation between samples explained 92% of the total variance, and only 8% of the variance was due to within-sample variation. In the second test (B), 99% of the variance was due to differences between samples and less than 1% due to within-sample variation.

3.5 | Associations between WKS, FDK and DON content

Correlation coefficients between the two traits evaluating *Fusarium* symptoms on grains, WKS and FDK, were significant and in a similar range for the three kernel sets ($r = 0.79$, $r = 0.77$ and $r = 0.81$, for BW1, BW2 and TRIT, respectively, Table 3).

DON content varied greatly between the sample sets, and for given WKS and FDK values, samples from BW1 presented a higher DON content than samples of BW2 and TRIT (Figure 10). The same severity of visible *Fusarium* symptoms on grains (evaluated by either FDK or WKS) was not necessarily associated with the same mycotoxin content, particularly between the three series. Despite that, within each of the three sample sets correlation coefficients between DON content and WKS and between DON content and FDK were all significant (Table 4). The samples of BW2 showed the highest correlation coefficients ($r = 0.86$ and $r = 0.83$), followed by the samples of BW1 ($r = 0.73$ and $r = 0.70$) and by TRIT ($r = 0.61$ and $r = 0.54$, for WKS-DON and FDK-DON, respectively). The comparison of the WKS-DON correlation with the FDK-DON correlation revealed no significant differences for the three kernel sets (Table 4). Correlations between WKS and DON content are therefore in a similar range as the ones observed between FKD and DON content.

4 | DISCUSSION

Breeding of FHB-resistant cultivars requires screening large numbers of experimental lines to identify improved cultivar candidates. Tools for high-throughput and low-cost measurement of FHB severity could enhance resistance selection. The newly defined trait, WKS and the quantification method described here, appears as a fast, easy

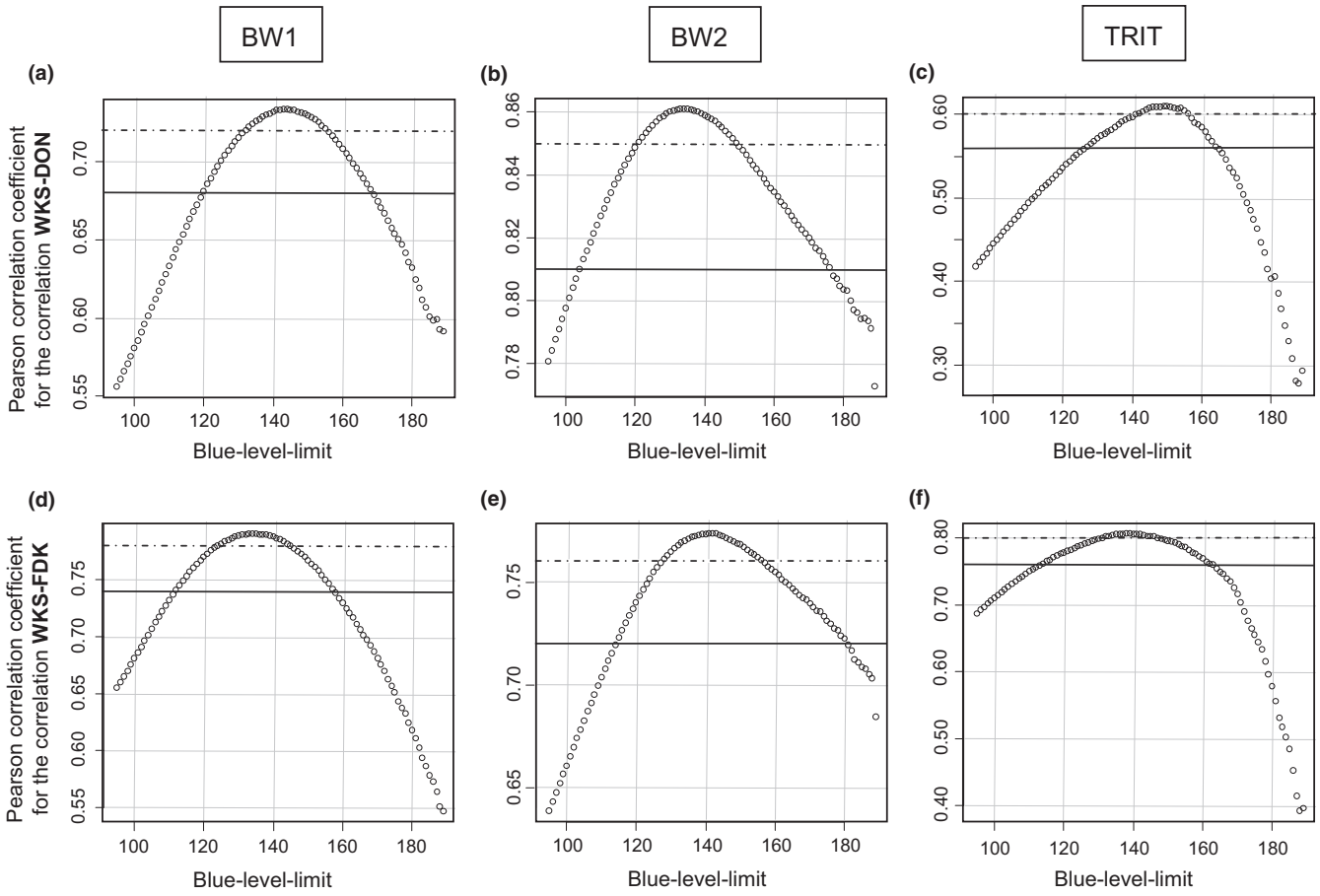

FIGURE 7 Evolution of the WKS-DON correlation as a function of the blue-level-limit for: (a) the kernel set BW1; (b) the kernel set BW2; (c) the kernel set TRIT. Evolution of the WKS-FDK correlation as a function of the blue-level-limit for: (d) the kernel set BW1; (e) the kernel set BW2; (f) the kernel set TRIT. The blue-level-limits which surpassed an acceptable correlation coefficient in a relaxed and in a strict sense are marked by solid lines and dashed lines, respectively. They mark a decrease of the correlation coefficient, in comparison with the maximum, smaller than 0.05 and 0.01, respectively

TABLE 3 Optimal blue-level-limits and acceptable[a] blue-level-limits determined for optimizing the correlation between WKS and FDK

	Blue-level-limit		Pearson[b] (WKS-FDK)	
BW1	Optimal	134	0.79	$p < 0.0001$
	Strict sense[a]	122–147	0.78	
	Relaxed sense[a]	111–158	0.74	
BW2	Optimal	141	0.77	$p < 0.0001$
	Strict sense[a]	126–159	0.76	
	Relaxed sense[a]	113–182	0.71	
TRIT	Optimal	138	0.81	$p < 0.0001$
	Strict sense[a]	128–151	0.80	
	Relaxed sense[a]	112–163	0.76	

[a]A blue-level-limit is considered as acceptable in a relaxed sense when the value of the coefficient of correlation was less than 0.05 lower than the maximum value observed. The blue-level-limit is considered as acceptable in a strict sense when this diminution was less than 0.01 to the maximum value. [b]Pearson correlation coefficient with associated *p*-value

and cost-efficient method for screening large numbers of grain samples. The method fits the needs of breeders to identify genotypes with higher levels of FHB resistance.

WKS is an evaluation of kernel whitening based on measuring the blue-level of grain pixels. We found a blue-level-limit of 140 appropriate to distinguish pixels representing Fusarium-damaged grain area from healthy grain area in two wheat and one triticale sets evaluated in this study. However, three kernel sets are possibly not a sufficiently large basis for setting this blue-level-limit as a universal standard. Optimal blue-level values may also depend on the specific grain samples under investigation, the used lamps, the camera or the setup of the photo studio. Therefore, re-calibration to obtain an appropriate blue-level-limit is recommended. The tests performed in our study showed that a moderate number of about 20 samples with carefully determined FDK values were sufficient to obtain an optimal blue-level-limit for WKS measurement, that maximized the correlation between WKS and FDK as well as between WKS and DON content.

TABLE 4 Optimal blue-level-limits and acceptable[a] blue-level-limits determined for optimizing the correlation between WKS and DON

	Pearson[b] (FDK-DON)		Blue-level-limit		Pearson[b]		Test HW[c] (WKS-DON)
BW1	0.70	$p < 0.0001$	Optimal	143	0.73	$p < 0.0001$	n.s. WKS~FDK
			Strict sense[a]	130–157	0.72		n.s. WKS~FDK
			Relaxed sense[a]	119–167	0.68		n.s. WKS~FDK
BW2	0.83	$p < 0.0001$	Optimal	135	0.86	$p < 0.0001$	n.s. WKS~FDK
			Strict sense[a]	118–152	0.85		n.s. WKS~FDK
			Relaxed sense[a]	103–178	0.81		n.s. WKS~FDK
TRIT	0.54	$p < 0.001$	Optimal	149	0.61	$p < 0.0001$	n.s. WKS~FDK
			Strict sense[a]	139–157	0.60		n.s. WKS~FDK
			Relaxed sense[a]	125–165	0.56		n.s. WKS~FDK

Note. n.s.: non-significant.

[a]A blue-level-limit is considered as acceptable in a relaxed sense when the value of the coefficient of correlation was less than 0.05 lower than the maximum value observed. The blue-level-limit is considered as acceptable in a strict sense when this diminution was less than 0.01 to the maximum value. [b]Pearson correlation coefficient with associated *p*-value. [c]Hotelling–Williams test to compare the significance of the difference between the correlation coefficients of FDK-DON and WKS-DON.

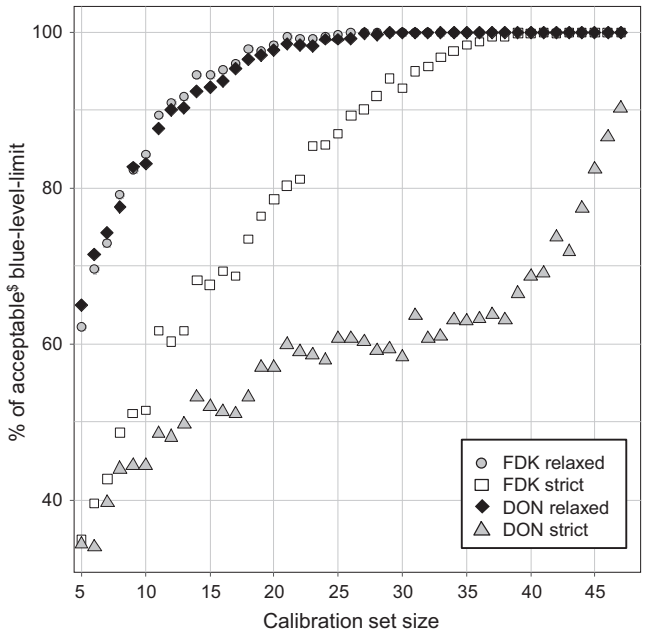

FIGURE 8 Association of the number of samples with measured FDK values used for calibrating the blue-level-limit for WKS determination (x-axis) with the accuracies of the obtained calibrations to predict FDK and DON (y-axis) in cross-validations. The y-axis represents the % of cases when the correlation WKS-FDK or WKS-DON was acceptable in a relaxed or a strict sense, respectively. See text for details. $A blue-level-limit is considered acceptable in a relaxed sense when the value of the coefficient of correlation was less than 0.05 lower than the maximum value observed. The blue-level-limit is considered as acceptable in a strict sense when this diminution was less than 0.01 to the maximum value

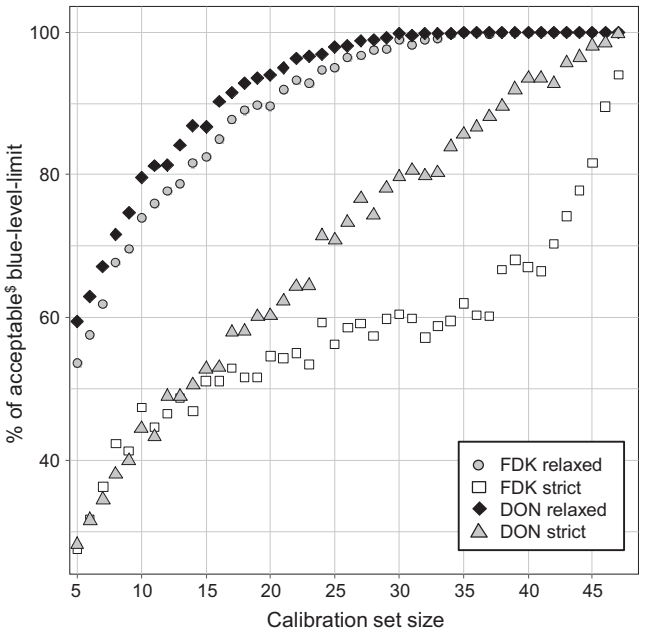

FIGURE 9 Association of the number of samples with measured DON content used for calibrating the blue-level-limit for WKS determination (x-axis) with the accuracies of the obtained calibrations to predict FDK and DON (y-axis) in cross-validations. The y-axis represents the % of cases when the correlation WKS-FDK or WKS-DON was acceptable in a relaxed or a strict sense, respectively. See text for details. $A blue-level-limit is considered acceptable in a relaxed sense when the value of the coefficient of correlation was less than 0.05 lower than the maximum value observed. The blue-level-limit is considered as acceptable in a strict sense when this diminution was less than 0.01 to the maximum value

WKS appears as a reliable tool to quantify FHB severity on infected grain samples in comparison with other measurements such as FDK or DON content. The coefficients of correlation between WKS-FDK and WKS-DON found in the two sets of bread wheat kernels were in a similar range as those reported for other optical methods. Hyperspectral imaging techniques showed a correlation coefficient of $r = 0.84$ between the optical measure and DON content (Barbedo et al., 2015). Near-infrared spectroscopic (NIR)

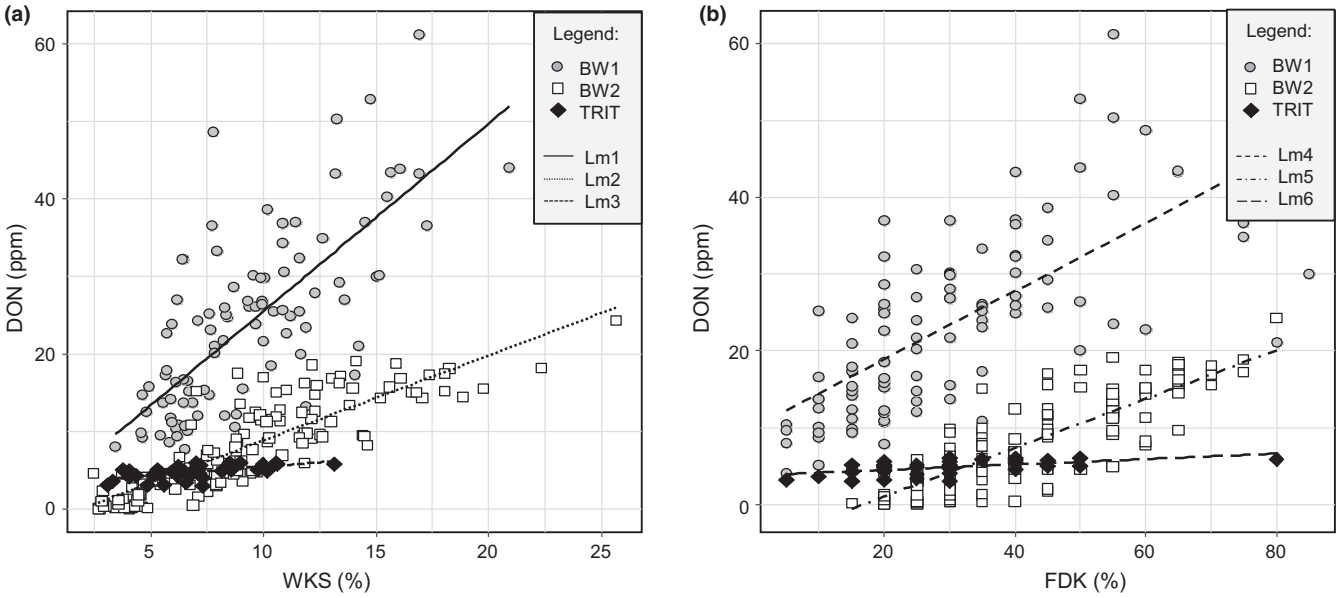

FIGURE 10 (A) DON content as a function of WKS for the three kernel sets. WKS was calculated for a blue-level-limit of 140. Lm1, Lm2 and Lm3 illustrate linear regressions for the model DON~WKS, with respective adjusted R-square of 0.53 ($p < 0.0001$), 0.74 ($p < 0.0001$), 0.34 ($p < 0.0001$), for the kernel sets BW1, BW2 and TRIT; (B) DON content as a function of FDK for the three kernel sets. Lm4, Lm5 and Lm6 illustrate linear regressions for the model DON~WKS, with respective adjusted R-square of 0.48 ($p < 0.0001$), 0.69 ($p < 0.0001$), 0.27 ($p < 0.0001$) for the kernel sets BW1, BW2 and TRIT

measurement performed on single kernels was strongly correlated with DON content ($r = 0.87$, Peiris et al., 2010). However, the correlation with the DON content was severely reduced when this method was applied on kernel sets ($r = 0.46$), although the correlation with FDK remained high ($r = 0.72$, Jin et al., 2014). In previous RGB analyses, where RGB parameters were considered globally on the image, the correlation between DON content and digital notations was only moderate ($r = 0.35$, Jirsa & Polišenská, 2011). With pixel per pixel analyses, similar levels of correlation as the ones we report in this study have been observed between FDK and the digital evaluation of the symptoms in two bread wheat kernel sets ($r = 0.80$ and 0.72, Maloney et al., 2014). Maloney et al. (2014) based the segregation between healthy and Fusarium-damaged pixels on a saturation-level-limit while in our study we applied a blue-level-limit. Both segregation processes are closely related as in the hues associated with kernels, variations in saturation are mainly due to variations in the blue-level. WKS is a competitive approach for quantifying FHB severity on infected grain samples. Our method for its automated assessment through RGB analysis requires only basic equipment and the pixel sorting process, as described in this publication, can easily be implemented into a computer algorithm in Python or in other programming languages such as JAVA or C++.

To perform visual FDK scorings, the assessor has to estimate the proportion of Fusarium-damaged kernels typically by comparing to exactly counted control samples. The "human factor" may impede the accuracy of FDK scorings. By contrast, WKS measurement is a standardized procedure, which avoids the inter-person variability and does not require sophisticated training or expertise. These advantages give timing and labour management a lot of flexibility. On the other hand, WKS scoring rests on colour features. One potential problem related with kernel scoring arises when samples with different natural grain colour must be evaluated. In the case of visual FDK evaluation, the assessor can intuitively recalibrate his/her visual notation to avoid attributing naturally light-coloured kernels as Fusarium damaged. With WKS measurement, this potential problem may be avoided by carefully setting the blue-level-limit high enough in order not to count naturally light-coloured kernels as infected. When the samples under evaluation display very large variation in natural grain colour, allocating the samples into subsets is recommended in order to determine an appropriate blue-level-limit for each subset.

Shrivelling and white to pale pink discoloration of grains are well known as typical symptoms of FHB infection, while WKS measurement rests on pixel whitening only. The high levels of correlation observed between WKS and FDK show that the assessment of kernel whitening is sufficient to quantify FHB severity on grain for infections caused by *Fusarium graminearum* and/or *F. culmorum*. This simplification in symptom evaluation is reliable for samples coming from inoculated experiments where kernel whitening is induced by Fusarium head blight infection. In the same way as FDK, WKS appears as a suitable method to assess resistance to kernel infection, also termed type IV resistance (Mesterhazy et al., 1999).

Artificially inoculated experiments usually reach higher disease severities on grains than those observed in conventional cereal production on farmer's fields. In inoculated experiments, correlation coefficients of FHB severity on grains measured by, *for example*, FDK (Paul et al., 2005) or WKS (our study) to DON are typically high and positive. However, an accurate prediction of the DON content in samples based on indirect measures such as field scores (Paul,

Lipps, & Madden, 2006), hyperspectral imaging (Barbedo, Tibola, & Lima, 2017) or WKS (this study) is unrealistic. For example in a meta-analysis using data from 126 studies comparing regression coefficients between field scores and DON content, the between-study variances for slope and intercept were significantly different from zero (Paul et al., 2006). Also the relationship between Fusarium damage on grains and DON content may be unequivocal, some kernels may appear asymptomatic and contain DON and vice versa (Barbedo et al., 2015, 2017). The relationship between Fusarium symptom severity and DON is influenced by environmental conditions (Paul et al., 2006), and the dominating Fusarium species or strains (Mesterházy et al., 2005). Despite that, using indirect scorings or measurements of FHB severity on grain samples for ranking samples for DON content is highly meaningful. Plant breeders aim primarily at ranking their breeding lines in order to select the most promising ones from their breeding population, rather than measuring exact DON values. The comparable correlation coefficients between FDK-DON and WKS-DON found in this study suggest that digital WKS measurement is a competitive alternative to visual FDK scorings for this purpose. The efficiency of indirect selection depends on the genetic variation of the target trait (*e.g.*, DON content) and the genetic correlation between the target trait and the trait under selection (*e.g.*, WKS), the heritability coefficient of the trait under selection and the selection intensity (Bernardo, 2010). For example, by selecting the best 20% of lines based on WKS values, the selected groups have on average 43% and 61% lower WKS values compared to the means of the unselected sample sets in sets BW1 and BW2, respectively. The same group of lines based on selection for low WKS comprises an even higher average reduction in DON content relative to the mean of the unselected population of 46% and 85% in the sample sets BW1 and BW2, respectively. This underlines that a substantial gain by selection in the target trait (reduced DON content) is achievable by selecting for breeding lines with low WKS values. Evaluation of symptoms on grains using WKS is therefore particularly suitable for pre-evaluating and selecting breeding lines with lower risk of kernel infection and the concomitant mycotoxin contaminations.

The pixel sorting process based on a blue-level-limit presented in this study allows reliable quantification of FHB symptoms on grains in both bread wheat and triticale. This scoring method may be extended to other cereal crops such as durum wheat, rye or barley, and more complex approaches for the pixels sorting based on machine-learning algorithms may even enhance the accuracy of the scorings, but have not been explored here. Measuring WKS is fast, requires typically half a minute per sample and has the additional advantage of avoiding the "human factor" and the subjectivity inherent to visual scorings. Taking digital images can be performed with basic equipment, and the automatized pixel sorting process can run for instance overnight without monopolizing the RAM of the computer during the day. The scoring procedure described here allows assessing resistance to kernel infection on many samples in an easier and less tiring way than FDK scoring. In addition, we demonstrate that WKS is as efficient as FDK to identify breeding lines with low risk of DON contamination. We propose WKS as a novel tool, suitable to research and breeding programmes, to score FHB disease symptoms on grains for large numbers of samples.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

MO designed the overall project, analysed the data and wrote the manuscript under the supervision of OR, EG, JLH and HB; MO, VT, ANB, ZLB, SD performed phenotyping; EG, JLH and HB edited and revised the manuscript. OR, EG, JLH, HB obtained funding. All authors, at the exception of OR, reviewed and approved this submission.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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PUBLICATION 2

TITLE

QTL mapping and successful introgression of the spring wheat derived QTL *Fhb1* for Fusarium head blight resistance in three European triticale populations

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ABSTRACT

Fusarium head blight (FHB) is a major problem in cereal production particularly because of mycotoxin contaminations. Here we characterized the resistance to FHB in triticale breeding material harboring resistance factors from bread wheat. A highly FHB resistant experimental line which derives from a triticale × wheat cross was crossed to several modern triticale cultivars. Three populations of recombinant inbred lines were generated and evaluated in field experiments for FHB resistance using spray inoculations during four seasons and were genotyped with genotyping-by-sequencing (GBS) and SSR markers. FHB severity was assessed in the field by visual scorings and on the harvested grain samples using digital picture analysis for quantifying the whitened kernel surface (WKS). Four QTL with major effects on FHB resistance were identified, mapping to chromosomes 2B, 3B, 5R and 7A. Those QTL were detectable with both *Fusarium* severity traits. Measuring of WKS allows easy and fast grain symptom quantification and appears as an effective scoring tool for FHB resistance. The QTL on 3B collocated with *Fhb1* and the QTL on 5R with the dwarfing gene *Ddw1*. This is the first report demonstrating the successful introgression of *Fhb1* into triticale. It comprises a significant step forward for enhancing FHB resistance in this crop.

KEY MESSAGE

The spring wheat derived QTL *Fhb1* was successfully introgressed into triticale and resulted in significantly improved FHB resistance in the three triticale mapping populations.

KEYWORDS

triticale; Fusarium head blight; resistance breeding; WKS; QTL; marker; GBS; SSR; *Fhb1*; *Ddw1*;

AUTHOR CONTRIBUTION STATEMENT

MO analyzed the data and wrote the manuscript under the supervision of OR, EG, JLH and HB; ML provided the inocula. MO, VT, ANB, ZLB, and SD collected phenotypic data; EG, JLH and HB edited and revised the manuscript. OR, JLH, HB initiated the study and obtained funding. All authors, at the exception of OR, reviewed and approved this submission.

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INTRODUCTION

Fusarium head blight (FHB), caused mainly by *Fusarium graminearum* and *Fusarium culmorum* (Bai & Shaner, 1994, 2004; Mesterházy et al. 2005; Ruckenbauer et al. 2001; Schroeder & Christensen 1963), is considered a disease of major importance in most areas of the world where wheat and other small grain cereals are grown. FHB can infect all members of the *Gramineae* and may significantly damage cereal crop within a few weeks after flowering (McMullen et al. 1997; Parry et al. 1995; Windels 2000). In addition to yield losses the contamination of the harvest by secondary fungal metabolites, known as mycotoxins, can devalue or even render the crop unsuitable for food and feed uses (D'Mello et al. 1999; Desjardins 2006; Kotowicz et al. 2014; Mesterházy et al. 1999; Windels, 2000). Mycotoxin contaminations in cereals for downstream processing, such as milling, production of bio-ethanol or brewing, are even more crucial since toxins tend to concentrate in the by-products, such as bran and distiller's dried grains with solubles (DDGS) that are commonly used as animal feed (Pinotti et al., 2016). Among the numerous Fusarium mycotoxins, deoxynivalenol (DON) and its derivatives are the most prevalent ones (Joffe 1986; Rotter 1996). They are harmful to both humans and livestock when ingested (Ghareeb et al. 2015, Gilbert & Tekauz 2000; Sobrova et al. 2010). Numerous countries have established guidelines or regulations for maximum DON content in cereals and cereal products in order to ensure the safety of food and feed (Van Egmond & Jonker 2004). As an example, the European authorities have set a limit of 1.25 mg/kg DON in unprocessed cereals other than durum wheat, oats and maize (Commission Regulation (EC) No. 1126/2007). Limiting Fusarium head blight development is the key for reducing mycotoxin contamination in cereal products. Chemical control measures are only partly effective in controlling *Fusarium* in small grain cereals (Mankeviciene et al. 2008; Šíp et al. 2010; Stack 2000), and the use of FHB-resistant cultivars combined with appropriate crop management practices is considered the most efficient method for managing this disease (Buerstmayr et al. 2009; Parry et al. 1995). Therefore, breeding cereal cultivars which are resistant to FHB and to the associated mycotoxin contaminations plays a crucial role for an integrated and sustainable management of this disease.

Genetic resistance to FHB in small grains is non-race specific, quantitatively inherited *i.e.* controlled by several genes with effects ranking from low to high and has a moderate to high heritability depending on population (Bai & Shaner 1994, Van Eeuwiik et al. 1995). Several types of mechanism underlying the genetic resistance have been described (Mesterházy 1995; Mesterházy et al. 1999; Miller et al. 1985; Schroeder & Christensen 1963). Resistance to initial infection (type 1) and resistance to fungal spread from an infected floret along the rachis (type 2) were first described by Schroeder and Christensen (1963). The overall FHB resistance is termed 'FHB severity in field' in this publication. It is assessed by evaluating the proportion of infected spikelets on a whole plot basis after spray inoculation and is considered to reflect the genotypic response during natural epidemics. The number of infected spikelets can be directly correlated with the number of damaged kernels. Some genotypes can however show invasion of seeds without visible sign of damage on hulls (Schroeder & Christensen 1963). Scoring for additional types of resistance is therefore of high interest. Resistance to deoxynivalenol (DON) accumulation, also known as type 3 resistance (Miller et al. 1985) is of particular interest for breeding. Several methods exist to directly quantify the DON content of a grain sample (Koch 2004; Krska et al. 2007; Maragos & McCormick 2000; Saccon et al. 2017; Sinha et al. 1995). Determination of toxin content is, however, expensive and therefore scarcely performed on large sample numbers in breeding programs. Breeders favor instead visual scorings to estimate the proportion of Fusarium damaged kernels (FDK) also known as type 4 resistance (Mesterházy 1995). Previous studies have shown that the correlation between DON content and the proportion of FDK in a grain sample is generally higher than the correlation between DON content and FHB severity observed on spikes in the field (Buerstmayr & Lemmens 2015; Paul et al. 2005, 2006). Infected grains can be visually differentiated from healthy ones, because they tend to be smaller, shriveled and white to pale pink colored (Abramson et al.1987; Mesterházy et al. 2005; Ruckenbauer et al. 2001). Although FDK is a widely used method, its scoring by visual inspection is subjective, time consuming, and labor intensive. Instead of performing visual evaluations of the damaged kernels, measurements using digital image analysis have shown great promise, such as quantifying the whitened kernel surface (WKS). WKS was recently suggested as a fast, easy and reliable measurement of

FHB severity on grains through digital picture analysis. Correlations between WKS and FDK are high, and correlations between WKS and DON content are in the same range as between FDK and DON content (Ollier et al. 2018).

Aside from the above-described resistance mechanisms, plant height, ear morphology, or earliness can also significantly influence resistance to FHB (Buerstmayr et al. 2011, 2012; Draeger et al. 2007; Kalih et al. 2014; Klahr et al. 2007; Mesterházy 1995; Paillard et al. 2004; Schmolke et al. 2008, Steiner et al. 2019; Boeven et al. 2016; Miedaner et al. 2017). The widely deployed Norin 10 semi-dwarfing *Rht* alleles, namely *Rht-B1b* and *Rht-D1b*, have been found associated with increased FHB susceptibility in bread wheat (Hilton et al. 1999; Mao et al. 2010; Miedaner & Voss 2008), and in durum wheat (Buerstmayr et al. 2012; Prat et al. 2017). Similarly, the dwarfing allele of the *Ddw1* gene commonly deployed in triticale germplasm and located on the rye chromosome 5R (Korzun et al. 1996) has been found to be related with increased FHB susceptibility in triticale (Kalih et al. 2014).

Triticale (x*Triticosecale* Wittmack) is the intergeneric amphidiploid between the female parent wheat (*Triticum* ssp.) and the male parent rye (*Secale* ssp.) with the first commercial varieties being released in the 1970s. Modern commercial varieties of this man-made crop have a genomic constitution of AABBRR with 2n = 6x = 42 chromosomes (Oettler 2005). They combine the high yield potential and good grain quality of wheat with winter hardiness and adaptation to unfavorable soils of rye (FAO 2004). Most of the produced grain is used on-farm as a feed grain, although triticale has shown great potential in bio-fuels (ethanol), organic and industrial chemicals, paper, the building and plastic industries and the beverage (beer) industry (FAO 2004). In 2017, it was cultivated on about 3.5 million ha in Europe where Poland, Belarus, Germany, and France are the main producers with 73% of the total European triticale acreage (FAOSTAT 2019). Triticale has shown high levels of disease resistance in the past, although with the increasing acreage in recent years FHB has become an important issue for farmers especially for pig and poultry production due to the risk for livestock of being fed with contaminated triticale grain (Goral et al. 2002; Murugesan et al. 2015; Pierron et al. 2016). The resistance of modern triticale varieties against FHB ranges approximately between its original parents wheat and rye (Kiecana et al. 1987; Langevin et al.

2004; Miedaner et al. 2001), allowing genetic improvement via resistance breeding by recurrent selection (Miedaner et al. 2004; Oettler & Wahle 2001). Winter triticale appears on average less susceptible to head blight than bread wheat, but there are large differences in resistance between specific triticale genotypes and even highly FHB susceptible triticale cultivars have been observed. This shows that studies on resistance of winter triticale should be conducted to preserve triticale's reputation as a 'healthy crop' (Goral et al. 2002). However, relatively few studies have been conducted to understand FHB resistance in triticale and to elucidate its genetic architecture (Dhariwal et al. 2018; Galiano-Carneiro et al. 2019; Kalih et al. 2014, 2015; Miedaner et al. 2016). On the other hand, the different kinds of genetic resistance to FHB are relatively well characterized for bread wheat (Buerstmayr et al. 2009). Since most of the identified QTL are located on the A and B genomes (Buerstmayr et al. 2009; Liu et al. 2009; Löffler et al. 2009), bread wheat represents a promising reservoir of resistance for triticale. Interspecific hybridization between wheat and triticale is furthermore a reliable method for transferring genetic information from one species to another and has been used to improve the resistance or the agronomic features of both crops, triticale and wheat (Hills et al. 2007; Lukaszewski & Gustafson 1983; Oettler 2005; Saulescu et al. 2011). The introgression of FHB resistance QTL from bread wheat into the genetic background of triticale could therefore be a promising strategy to broaden the genetic diversity of resistance factors in elite triticale germplasm.

Among the QTL for FHB resistance identified in bread wheat, those on chromosomes 3BS (*Fhb1*) and 5AS (*Qfhs.ifa-5A*) are the most prominent ones (Buerstmayr et al. 2009). Both derive from the well-known resistance donor Sumai-3 (Buerstmayr et al. 1999; Waldron et al. 1999). *Fhb1* is a well-characterized QTL which has been validated in numerous studies and confers a high level of FHB resistance to fungal spreading (type 2 resistance) (Agostinelli, et al. 2012; Anderson et al. 2001; Balut et al. 2013; Bourdoncle & Ohm 2003; Buerstmayr et al. 2002, 2003; Chen et al. 2006; Cuthbert et al. 2006; Jiang et al. 2007; McCartney et al. 2007; Prat et al. 2017; Shen et al. 2003; Waldron et al. 1999). *Qfhs.ifa-5A*, on the other hand, has been shown mainly to increase resistance to initial infection (type 1)

(Buerstmayr et al. 2003; Lin et al. 2006; Xue et al. 2011) and is tightly associated with high anther extrusion in bread wheat (Steiner et al. 2019).

The impact of these two major QTL on FHB resistance in triticale has however not been investigated until now. For this purpose, three related mapping populations were generated by crossing an FHB-resistant triticale pre-breeding line possessing *Fhb1* and *Qfhs.ifa-5A* with two current triticale cultivars and one F1 hybrid. These mapping populations were evaluated in replicated field trials under *Fusarium* inoculation in order to map, quantify and validate stable QTL for FHB resistance in the genetic background of modern triticale.

The aims of this study were thus (i) to get further insight into the genetic architecture of FHB resistance in triticale, (ii) to examine the effect of *Fhb1* and *Qfhs.ifa-5A* in triticale genetic backgrounds and show the value of introgressing wheat resistance factors in elite triticale germplasms, (iii) to investigate the association of plant height and FHB resistance with specific focus on the dwarfing gene *Ddw1*, (iv) and finally, to evaluate, in a breeding context, the potential of the WKS, a new method of FHB symptom measurement on grains by digital picture analysis.

MATERIAL AND METHODS

Plant materials

Three related mapping populations were developed from crosses between the FHB resistant triticale line G8.06 and three triticale cultivars Tulus (T), Elpaso (E), and the F1 of Agostino × Grenado (AG), respectively. The crosses were carried out by Dr. Herbert Bistrich from the breeding company Saatzucht-Donau GesmbH (Austria). F_2 populations were returned to IFA-Tulln, and advanced to the F_4 generation by single seed descent without intended selection. Seeds descending from single F_4 spikes were bulk propagated and used as $F_{4:5}$ lines for field tests in 2014 and 2015. $F_{4:5}$ lines were propagated in microplots in 2015 and $F_{4:6}$ lines used for the field trials in 2016 and 2017. Tulus is a variety bred by Nordsaat Saatzucht GmbH (Germany) and registered in 2008. Agostino is a variety bred by Lantmaennen SW Seed B.V. (Netherland) and registered in 2009. Elpaso and Grenado are both varieties bred by DANKO Hodowla Roslin sp. z o.o. (Poland) and registered in 2010 and 2004, respectively. Santop is a variety bred by Saatzucht Dr Hege GbRmbH (Germany) and registered in 1998. The triticale pre-breeding line G8.06 was developed at IFA-Tulln (Austria) through two generations of marker-assisted backcrossing of the highly FHB-resistant spring wheat line CM-82036 (Sumai-3 x Thornbird-S), which possesses the FHB resistance QTL *Fhb1* and *Qfhs.ifa-5A* (Buerstmayr et al. 2002, 2003) into the background of the triticale cultivar Santop (Hege Seeds, Germany). Line G8.06 was selected among ten BC2-lines as the one with the highest and most consistent level of FHB resistance in replicated field trials (data not shown). One hundred twenty $F_{4:5}$ lines from each of the three populations were sown in the field and evaluated for *Fusarium* resistance and flowering time in 2014. Among those descendants, 92 lines were chosen from populations T and E, and 91 from population AG for QTL mapping. Selection criteria were set to represent the whole range in FHB severity but avoiding visibly heterogeneous and very early and very late flowering lines. The objective was to keep the populations diverse for FHB symptom severity and to reduce the diversity in flowering time.

Field trial and *Fusarium* infection

The three mapping populations and the parental lines were tested in repeated *Fusarium* inoculated field experiments at IFA-Tulln, Austria (48°19'05"N 16°04'08"E, 177 m above sea level) during four growing seasons from 2014 to 2017. Temperature and precipitation during each trial year are shown in Online resource 1. Experiments were laid out in randomized complete block design with two blocks per population. Plots consisted of double rows of 1 m length and 17 cm spacing. Sowing time was late October to early November in each season. The two blocks were sown two weeks apart. These staggered sowing dates led to slightly different flowering dates between the blocks. Management of the field trials was conducted following good agronomical practice as described in Buerstmayr et al. (2002). All experiments were spray inoculated with a motor-driven backpack sprayer in the late afternoons. The DON producing *F. culmorum* isolate IFA104, at a conidial concentration of 5.0×10^4 ml^{-1}, was used in 2014 and 2015, and the isolate Fc91015, at a conidial concentration of 2.5×10^4 ml^{-1}, was used in 2016 and 2017. Inoculations were performed within each block on all plots, when 50% of the plants in the earliest plot of a block reached anthesis. Inoculations were repeated at 2-days intervals and ended 2 days after the last plot of the block flowered, resulting in up to six inoculum applications per block. At each inoculation cycle, about 100 $ml.m^{-2}$ of conidial suspension was sprayed onto the triticale heads. Inoculum suspension was prepared by using the protocol described in Buerstmayr et al. (2000). Aliquots of conidia stock solutions were stored at −80 °C then thawed at 37 °C and diluted with tap water to achieve the desired final spore concentration just prior to inoculation. An automatic mist-irrigation system, switched by leaf-wetness measurement, maintained humidity and kept the plants wet for 20 h after inoculation to facilitate spore germination and infection.

FHB resistance scoring

FHB severity was visually estimated as the percentage of infected spikelets within each plot on days 10, 14, 18, 22 and 26 after anthesis. The area under the disease progress curve (AUDPC) was calculated and used as an integrated measure of the overall disease severity as described by Buerstmayr et al. (2000). Plant height (PH) was measured in centimeters from the soil surface to the tip of the head, excluding awns

and the date of flowering was recorded and converted into days after May 1st (Dmay) for all experimental plots.

Fusarium symptoms on grains were digitally assessed using the whitening kernel surface (WKS) trait evaluation as described in detail in Ollier et al. (2018) (Online resource 2). All plots were harvested at full ripening, using a plot combine harvester (Wintersteiger Nursery Master) set to low wind speed to avoid or reduce the loss of light-weight infected kernels. Twenty grams of grain from each seed sample were poured in bulk on a blue tinted paper and photographed under standardized light conditions. The red, green and blue levels of each pixel (RGB levels) within a picture were analysed using a script written in Python (Python Software Foundation, Inc. Python Language Reference, version 3.4.1. Available at http://www.python.org). Pixels of each picture were separated into three categories based on their RGB levels: background, healthy grain, and diseased grain pixels. The WKS was evaluated as the percentage of diseased among all grain pixels. The differentiation between healthy and diseased kernel pixels was based on a blue-level-limit determined through calibration as described in Ollier et al. (2018). This level was set to 150 for the three populations and all the analyses presented in this publication.

Phenotypic data analysis

Statistical tests were performed for each population separately. A first analysis was performed for single experiments with a linear model of the form:

$$1)\ P_{ik}=\mu+G_i+R_k+e_{ik}$$

where P_{ik} is the phenotypic value, μ the population mean, G_i the effect of the i^{th} genotype treated as fixed, R_k the random k^{th} replicate effect, and e_{ik} the residual effect with $e \sim N(0, \sigma_e^2)$. A combined analysis across experiments was then performed by fitting the linear model:

$$2)\ P_{ijk}=\mu+G_i+E_j+E_j(R_k)+GE_{ij}+e_{ijk}$$

where P_{ij} is the phenotypic value, μ the population mean, G_i the effect of the i^{th} genotype, E_j the effect of the j^{th} experiment, $E_j(R_k)$ the effect of the k^{th} replicate nested within the j^{th} experiment, GE_{ij} the ij^{th} effect of the genotype-by-experiment interaction and e_{ijk} designates the residual.

Best linear unbiased estimates (BLUEs) for the AUPDC, WKS, plant height and flowering date of each line were derived from both models with experiment and replicate effects modeled as random, as was the genotype-by-experiment interaction, whereas the genotype effect was treated as fixed. Significance of genotypic effects were attested with both models and with all factors treated as fixed. For all statistical tests, the parental lines were excluded from the calculations. Finally, broad sense heritability coefficients for each trait were derived from both models with all effects set as random and were calculated according to Holland et al. (2003):

3) $H^2=\sigma^2_G/(\sigma^2_G +(\sigma^2_{GxE} /e)+ (\sigma^2_e /re))$

where σ^2_G denotes the genotypic variance, σ^2_{GxE} the genotype-by-experiment interaction variance, σ^2_e the error variance that were determined by the restricted maximum likelihood (REML) method, e indicates the number of experiments and re the total number of observation plots per line.

Statistical analysis was performed in R 3.3.2 (R Core Team 2016). All linear mixed and random models were fitted with the *lme4* package (Bates et al. 2015), while multiple comparisons of line means were performed with a Tukey´s range test as implemented in *agricolae* (Mendiburu 2015).

Genotypic data

Genomic DNA was extracted from fresh leaves of 10 pooled plants of each F_4 and parental lines using a CTAB-based procedure modified from Saghai Maroof et al. (1984). High-density genotyping of all individuals was performed using genotyping-by-sequencing (GBS) with the DArTseq platform (DArT PL, Canberra, Australia). The markers identified by the DArTseq assay included SNP as well as presence–absence variations (PAV) (Li et al. 2015). The markers were filtered based on a call rate ≥95%, and less than 20% missing data. For linkage map construction and QTL mapping of the AG population, which is a 3-way cross, only markers which were monomorphic among Grenado and Agostino (=homozygous) and polymorphic between Agostino/Greando and G8.06 were chosen. Markers showing significant segregation distortions ($p < 0.10$) were also discarded in all three populations. Finally, a total of 2216, 710, and 420 SNP were available for the T, AG, and E populations after quality filtering, while the number of PAV was slightly higher with 15124, 4092, and 6726 markers per population, respectively. In

addition, all F4 and parental lines were genotyped with four simple sequence repeat (SSR) markers, *gwm493* and *gwm533* (Roeder et al. 1998) linked to *Fhb1* (McCartney et al. 2004), and *barc180* and *barc56* (Song et al. 2005*)* linked to *Qfhs.ifa-5A* (Buerstmayr et al. 2002). The analysis of SSR marker was done as described by Steiner et al. (2004). Agostino, Grenado, G8.06 and the 91 F_4 of the AG population were finally genotyped with conserved ortholog set (COS) markers linked to the dwarfing gene *Ddw1* (Hackauf and Goldfisch pers. commun.).

Linkage maps constructionCross-specific linkage maps of the AG and E populations were constructed with all available markers, co-dominant SNPs and dominant PAVs. The software CarthaGene 1.2.3 (de Grivy et al. 2005) was selected to build the map due to its capacity to deal with dominant markers and with the residual heterozygosity in the F_4 lines. Robust linkage groups where constructed using a maximum two-point distance of 50.0 cM (Haldane), and a minimum two-point LOD of 15.0. The markers in common with the triticale map provided by Tyrka et al. (2015) and with the wheat consensus map version 4 provided by DArT PL (Diversity Arrays Technologies, personal communication, 2016), were used as reference points for assigning linkage groups to specific chromosomes. Markers were then ordered through the initial framework mapping command *buildfw*. This incremental insertion procedure was set with a keep and an adding threshold of 3.0 LODs, starting the build process from an empty map. Finally, the genetic distances between markers in centimorgan (cM) were calculated using the Kosambi mapping function.

The T-population displays 3 times more SNP markers than the two other populations. It was therefore possible to construct the cross-specific linkage map of this population based on SNP markers only and using the MSTmap algorithm (Wu et al. 2008) included in the R package ASMap V0.4 (Taylor & Butler 2015). The objective function was set to minimize the sum of recombination events between markers for map construction. Robust linkage groups where constructed using a p-value threshold set to 1×10^{-9} in a first step, and the assignment of the linkage groups to chromosome was done as described above by comparing the location of markers to markers from the triticale map provided by Tyrka et al. (2015) and the wheat consensus map version 4 provided by DArT PL (Diversity Arrays Technologies, personal

communication, 2016). Genotypic data was subsequently pooled on a chromosome basis and regrouped at a less stringent threshold using a p value of 1×10^{-6}. Genetic distances were calculated with the Kosambi mapping function.Consensus maps for the chromosomes 2B, 3B, 5A, 5R, and 7A, which appeared as of special interest in our study, were constructed across the three populations. All markers previously selected to construct the three cross-specific linkage maps and all additional high-quality SNP and PAV markers that were polymorphic in at least two populations were used. New marker ordering processes were run with CarthaGene 1.2.3 (de Grivy et al. 2005) for each population and each of these five specific chromosomes. The generated cross-specific linkage maps of the three populations were chromosome-wise merged, while ensuring that the ordering of the markers in the individual linkage maps is preserved by using the R-package LPmerge (Endelman & Plomion 2014). Genetic maps were finally drawn with MapChart (Voorrips 2002). QTL mapping

The calculated BLUEs from the analysis within individual experiments and across experiments were used for quantitative trait loci analyses that were performed for each trait separately. QTL mapping was first performed for each population individually with the previously described cross-specific maps by performing interval mapping and composite interval mapping via the multiple imputation method (Sen & Churchill 2001) as implemented in the R package *R/qtl* (Broman et al. 2003). The number of marker covariates was selected by a forward approach in the composite interval mapping, while setting a window size of 10 cM. LOD significance threshold for a type I error rate of $\alpha \leq 0.05$ were obtained for each trait and experiment based on a 1000 times replicated permutations test (Churchill & Doerge 1994), and significant QTL were subsequently fitted in a multiple QTL model. The existence of further QTL, the presence of QTL-by-QTL or QTL-by-genetic background interaction were tested by using the *addqtl*, *addint*, and *addpair* functions respectively (Broman et al. 2003). An ANOVA was conducted with the final multiple QTL model to estimate the proportion of the phenotypic variance explained by all terms in the model. The percentage of phenotypic variance explained by each QTL as well as their LOD scores were estimated by a Type III sum of squares test by dropping one QTL at a time and comparing the full

model to the model with the omitted term. Confidence intervals were finally defined for each QTL by calculating a 1.5-LOD support interval.

Thereafter, multi-parent population QTL mapping was realized to increase the power of QTL detection and compare the effects of QTL detected in cross-specific models (Blanc et al. 2006; Li et al. 2005). The combined analysis of the three related mapping populations was performed by using the methodology outlined by Garin et al. (2017) with a focus on the parental and bi-allelic models. A parental model assumes the contribution of one unique allele per parental line. In related populations, the contribution of each cross-specific parent may differ characterizing the relative instability of the QTL in different genetic backgrounds. A bi-allelic model is based on the identical by state (IBS) assumption of each SNP, assuming that the same marker score corresponds to the same allelic state. The bi-allelic model is therefore similar to models used for genome-wide association mapping and allows a global characterization of the QTL alleles based on all available information. The detection of QTL in related populations, with both, parental and bi-allelic models, is only possible for QTL with a relatively small QTL x background interaction. QTL were detected by performing simple interval mapping (SIM) and composite interval mapping (CIM) with both the parental and bi-allelic models with a homogeneous residual variance using the previously generated consensus map. For composite interval mapping a maximum of one cofactor was selected per chromosome when being above the significance threshold of $-\log_{10}$ (p-value) = 3. The threshold for declaring significance of a marker-trait association has been empirically determined by using the 95% quantile value from a null distribution representing the maximum genome-wide significance values obtained from 1000 permutations. The effects of the QTL alleles and the percentage of the phenotypic variance explained by each QTL were estimated using a linear model including all significant QTL position, whereas confidence intervals were defined for each QTL by calculating a 1.5 $-\log_{10}$ (p-value) drop-off interval.

Robustness of QTL were evaluated employing a 5-fold cross-validation (CV), replicated 20 times, following a modified algorithm of Utz et al. (2000) adapted to the multi-parent populations context (Garin et al. 2017). Briefly, five subsets were generated within each cross with one subset used as validation set

and the remaining subsets as training set at a time. The training set was used to detect QTL and the proportion of phenotypic variance explained by the detected QTL in the training set *pTS* was saved. The detected QTL and their estimated effects were then used to predict the phenotypic values of the validation set with *pVS* representing the square correlation between the predicted and observed phenotypic values. The bias was calculated by *1-(pVS/ pTS)* in order to get some insight into the stability of the estimated QTL effects. All multi-parent population QTL mapping analyses were performed with the R package *mppR* (Garin et al. 2017).

RESULTS

Trait variations and correlations

Table 1 summarizes mean values of the parents, means and ranges of the populations, least significant differences and broad-sense heritabilities for FHB severity in field (AUDPC) and on grains (WKS), plant height (PH) and flowering date, with variance component estimates available in Online resource 3. For all traits, significant genotypic effects were revealed, and continuous distributions were displayed within the three triticale populations, except for plant height in the AG population, which shown a bimodal frequency distribution (Fig. 1). The average FHB severity of the three populations was significantly lower in the E population than in the T, and AG populations, and the disease pressure was significantly different among years, with the 2016 experiment showing higher symptoms, followed by the 2014, 2017 and 2015 experiments. Transgressive segregation towards resistance was observed in all populations and was statistically significant for the T and AG populations, but not for the E one. Significant differences in plant height were observable among the parents of each population whereas no such differences were detected for flowering date. For both traits, no transgressive segregation was observed. Correlations between AUPDC and WKS ranged between r=0.61 and r=0.78 for the three populations. Plant height (PH) was positively correlated with both FHB resistance traits within the AG population, where taller plants showed significantly lower FHB severity. Correlations between plant height and FHB-resistance traits were lower in the T and E populations and did not exceed r=0.5. Correlation coefficients between FHB-resistance traits and flowering date remained very low and varied between r=-0.20 and r=0.39 without revealing a clear pattern (Table 2).

Linkage maps

The number of markers within maps for the T, AG, and E populations was reduced to 1036, 432 and 430 unique loci with total map lengths of 2908, 2666 and 4324 cM per population. The average marker distance amounted 2.7, 6.5 and 10.5 cM for the T, AG, and E populations respectively. Linkage groups were obtained for all chromosomes, except 7R and 2R for the T and AG populations, and 7R and 3R for the E population. Consensus maps built on the three populations for the chromosomes 2B, 3B, 5A, 5R and

7A contained between 68 and 104 markers with an average space between two markers between 1.6 and 4.7 cM. For reading ease, only selected markers are displayed together with the QTL mapping results (Online Resource 4), while more detailed information concerning all mapped markers and their positions can be found in Online Resource 5.

QTL analysis for flowering date and plant height

Multiple QTL for flowering date were detected with cross-specific models on 4A and 5R for the T population, 3A and 5R for the AG population, and 4A, 6B, and 7A for the E population (Table 3, Online Resource 4). Co-localization of QTL for anthesis date and plant height was found only on chromosome 5R in the AG population. The QTL mapped to marker positions *Xiac129* and *Xiac130* flanking the dwarfing gene *Ddw1*. In the AG population, this QTL accounted for 78% and 25% of the variation for plant height and flowering date respectively (Table 3), corresponding to an average height decrease of 28 cm and an average delay of flowering of 1 day. The use of a parental model, when performing an analysis on the three populations together with the consensus map, confirmed the effect of *Ddw1* in the AG population (Table 4). Additional QTL for plant height were detected with cross-specific models on 5A and 6A for the T population, 2B and 5A for the AG population, and 5A and 5B for the E population. The common parent G8.06 contributed the tall allele for all of them except for the QTL on 2B detected in the AG population (Table 3, Online Resource 4). Significant epistatic interactions were observed for the plant height QTL on 5R and 2B in the AG population, and for the 5A and 5B QTL in the E population, explaining 1.4% and 11.5% of the phenotypic variance in their respective populations (Table 3). Three different QTL, corresponding to three different positions, were characterized on chromosome 5A by the previously described parental model. The plant height QTL previously found on the chromosome 2B in the AG population was however not detected by the parental model.

QTL analysis for FHB severity in field and on grains

QTL for FHB severity (AUDPC and WKS) were detected with cross-specific models on 2B, 3B, 6A, 6B and 7B for the T population, 3B, and 5R for the AG population, and 6B and 7A for the E population. For

all these QTL, except the ones on 6B, the alleles from resistance donor parent G8.06 were associated with an increased FHB resistance (Table 5). Among all detected QTL, those on 2B and 3B for the T population, 3B and 5R for the AG population, and 7A for the E population explained the largest proportion of phenotypic variance in their respective populations and were detected in all years with both traits, AUDPC and WKS.

Markedly, the QTL detected on chromosome 3B mapped to marker positions *gwm493* and *gwm533*, which flank the position of the introgressed *Fhb1* locus from hexaploid wheat. *Fhb1* passed the significance threshold with cross-specific models across all experiments in the T and AG populations but not in the E one. The QTL was detected with both the parental and bi-allelic models (Table 6), and its stable effect was confirmed by cross-validation (Table 7), where it was significant in 96 out of 100 repetitions. Moreover, the higher detection power of the parental model allowed identifying a significant effect for *Fhb1* in all three populations, including the E population. The resistant allele of the QTL led to an average reduction of FHB symptom severity of 25%, 28%, 9% in field, and of 35%, 30%, and 8% on grains, for the T, AG, and E populations, respectively (Fig. 2, Online Resource 6). These substantial differences in the level of expression of the QTL among populations are characteristic for a QTL x genetic background interaction, which could partially be explained by the presence of epistatic interactions in this study. In the T population, a significant interaction was detected with the cross-specific model between *Fhb1* and the QTL on 7B. The genotypes carrying the G8.06 allele for both the 3B and 7B QTL were significantly more resistant than genotypes presenting other allele combinations. In the T population cross-specific model, this interaction explained 12% of the global phenotypic variance in field and 7% on grains.

The QTL *Qfhs.ifa-5A* from hexaploid wheat was also introgressed into the resistant triticale parent G8.06 and therefore segregating in all three mapping populations. However, none of the markers near this locus was found associated with FHB symptom severity with any of the tested models (Fig. 2, Online Resource 6).

The FHB-resistance QTL detected with cross specific models on chromosome 5R in the AG

population, mapped to marker positions *Xiac129* and *Xiac130* which flank the dwarfing gene *Ddw1*. In this population, it exibited a major effect on resistance with an average symptom severity reduction of 26% in field and of 31% on grains, with the tall allele enhancing resistance. The analysis performed on the three populations together with the consensus map and a parental model confirmed the effect of *Ddw1* in the AG population (Table 6), and the employed cross-validation tests showed an intermediate level of stability (Table 7) of this QTL which was significant in 47 out of 100 repetitions. No epistatic interaction was identified with this QTL, neither with the other QTL of the model, nor the genetic background.

Aside from these effects, two other QTL for FHB resistance were detected with a major effect, one on chromosome 2B, and another one on chromosome 7A. The marker *8514068*, in linkage disequilibrium with the QTL on chromosome 7A (Table 5), indicates that the line G8.06 would be the only parental line carrying the resistant allele for this QTL. However, the effect of the QTL was only significant with cross-specific models in the E population, where it resulted in a reduction in FHB severity of 22% on the heads in the field and of 18% on the grains (Table 5). Due to a lack of proximate markers in the chromosomal region of the 7A QTL in the consensus map, the MPP analysis did not detect this QTL. The major effect QTL detected on chromosome 2B was merely polymorphic in the T population where it led to a reduction in field severity of 26% and of 35% on the harvested grains. Epistatic interactions were identified between this QTL and another one of the cross-specific model positioned on the chromosome 6A (Table 5). By refining the analysis using both the bi-allelic and parental models, it was possible to localize this QTL in a reduced area of 1.3 cM on the consensus map, where the 2B QTL effect was further confirmed by cross validation (Table 7). When aligning the markers of the consensus and T population cross specific maps of this QTL interval on the wheat physical map, they were located in a 9.6 mega base pairs (Mbp) region containing 48 high confidence genes. A description of the genes contained in this area and the marker blasting information are summarized in Online Resource 7.

To illustrate the effects on FHB severity of combining *Fhb1* with other QTL with major effects on resistance, the lines of the T, AG and E populations were classified in subgroups according to their allele status at *Fhb1 and* the QTL on 2B for the T population, on 5R for the AG population, and on 7A for the E

population. Resistance level and plant height were compared among the different subgroups (Fig. 3, Online resource 8). In the T and AG populations, lines carrying both resistance QTL had significantly less disease severity than the lines carrying only *Fhb1* and in the AG population, lines carrying the dwarfing allele at *Ddw1* locus were significantly shorter and more susceptible than the ones harboring the wild-type allele.

DISCUSSION

FHB resistance is a top priority in cereal breeding and is receiving high attention ranging from basic research to cultivar development. Breeding and growing varieties that resist mycotoxin accumulation are of foremost importance for crops such as triticale, which are used primarily on the farm as animal feed, without checking for a potential mycotoxin contamination of the harvest. Additionally, triticale is a useful energy crop for bioethanol fermentation. The typical output of bioethanol production from cereals is, that about 1/3 of the cereal mass is converted into bioethanol, 1/3 is converted to CO_2, and 1/3 is the so-called stillage, which is normally dried to produce DDGS (Distiller's Dried Grains with Solubles) a co-product of the distillery industries. DDGS is used as high value protein feed and could, due to its optimal nutritional composition, partly replace even soygrist in pig fattening (Schedle et al. 2010). Due to the production scheme in bioethanol conversion, mycotoxin contaminations in the starting material are concentrated in the DDGS, by a factor 3 (Schaafsma et al. 2009).

However, relatively little research for FHB resistance has been conducted for triticale until now whereas genetic resistance in bread wheat has been well described. Three related populations between a triticale FHB-resistant donor line with *Fhb1* and *Qfhs.ifa-5A* introgressions from bread wheat, and two adapted triticale varieties and one F1 hybrid, were analyzed in this study. Analyzing three mapping populations with large variation in FHB severity, allowed further dissecting the genetic basis of FHB resistance in different elite triticale genetic backgrounds, and combined QTL detection with QTL validation. Considering the connectivity between these three related populations by using a parental model permitted comparing the effects of QTL detected in distinct cross-specific models, whereas the use of a bi-allelic model allowed a global characterization of the QTL effects based on all available information and finally improved the quality of their localizations.

Genetic architecture of FHB resistance in triticale

Even though the disease pressure was significantly different between the four years, no isolate-specificity was detected in the genetic architecture of the resistance when comparing the architecture observed in years 2014-2015 with the architecture observed in years 2016-2017. The high broad sense heritability

coefficients in the three populations indicate that a large proportion of the variation among line means was due to genetic differences. A total of 9 QTL with varying effects on FHB resistance were identified on chromosomes 2B, 3B, 5R, 6A, 6B, 7A, 7B confirming previous results about the quantitative inheritance of FHB resistance in triticale (Dhariwal et al. 2018; Galiano-Carneiro et al. 2019; Kalih et al. 2015; Miedaner et al. 2006; Oettler et al. 2004). Only one QTL was identified on the rye genome Except for the two QTL on the 6B, all resistant alleles descended from the common parent G8.06, which was pre-selected for its high resistance to FHB. Significant transgressive segregation was observed in all populations, suggesting the presence of additional resistance QTL which remained undetected, possibly due to the relatively small population sizes. Nevertheless, QTL with large effects are detectable even in rather small populations (Vales et al. 2005) and four QTL with major effect on the resistance to FHB were detected on chromosomes 3B, 2B, 7A and 5R.

One of the most promising marker-trait associations found in this study was the one identified on chromosome 3B, which mapped in the *Fhb1* region between the SSR markers *gwm493* and *gwm533*. The effects of *Fhb1* observed in our populations were in the same range as the ones previously observed in wheat. Buerstmayr et al. (2003) showed that *Fhb1* explained 20% of phenotypic variance in a spring wheat population, and Prat et al. (2017) reported that it explained 5-14% of the phenotypic variance in three durum wheat populations. In accordance with previous results (Agostinelli et al. 2012; Balut et al. 2013; Buerstmayr et al. 2009; Prat et al. 2017; Pumphrey et al. 2007; Verges et al. 2006), our study showed that the effect of *Fhb1* on improving FHB resistance is robust, but the magnitude may vary depending on the genetic background.

Aside from *Fhb1* two further QTL on chromosomes 7A and 2B both with major effect on FHB resistance were detected. Several FHB resistance QTL with large effect have been detected in bread wheat on these two chromosomes (Buerstmayr et al. 2009). In 2011, Jayatilake et al. reported a QTL from CS-Sumai 3-7ADSL with a high level of FHB resistance for symptom spread within a spike (type 2) and low deoxynivalenol accumulation in infected kernels (type 3). Designated as *Fhb7AC*, this QTL mapped near the centromere of the chromosome 7A and explained a similar level of resistance than the QTL detected in

this study on chromosome 7A (22% phenotypic variation for type 2 and 24% for type 3 resistance, Jayatilake et al. 2011). Further testing will be necessary to uncover whether or not those two QTL are identical or at proximity. Improvement in the mapping resolution may be a difficult task regarding the proximity with the centromere. The effect of the QTL detected on chromosome 7A in this study, was significant in the E population only, although the closest marker we found in linkage disequilibrium with the QTL (Table 5) indicates that this QTL segregates in all three populations. The cross-specific map built for the E population is 1.5 time larger than the ones of the T and AG populations. This situation did not allow a precise localization of the QTL on the chromosome 7A and a large physical distance may exist between the QTL and the closest marker. The importance of the QTL effect, associated with the many common markers between the E population map and the one provided by Tyrka et al. (2015), give us a reasonable level of confidence regarding the presence of this QTL on the chromosome 7A in the E population but the allele status of the lines Tulus, Agostino and Grenado is however dubious. The parental line El Paso may be the only one carrying the susceptible allele for this QTL, which would explain why the effect of the QTL is significant in the E population only. No report has been found in the literature of any large effect QTL in chromosome 2B coming from populations with Sumai-3 in their pedigree. The parental lines Tulus and Grenado carry the susceptible allele for the QTL on the 2B, which could explain why they were much more susceptible than the other parental lines Agostino, ElPaso and G8.06. Polymorphism at the QTL locus was detected in the T population only. However, cross validation results performed with multi-parental models, showed comparable level of stability when comparing with *Fhb1*, and both QTL presented similar additive effects in the T population.

The forth QTL with major effect on FHB resistance identified in this study was detected in the AG population, on chromosome 5R, at the exact position where markers linked to the *Ddw1* gene were mapped. It was the only FHB resistance QTL overlapping with QTL for flowering date and plant height. A large effect of this QTL on plant height and flowering time was previously described in rye and in triticale (Börner et al. 2000; Kalih et al. 2014), while the strong effect of *Ddw1* on FHB resistance was verified in Kalih et al. (2014). It accordingly explained 48%, 77% and 71% of the genotypic variance for

FHB severity, plant height and flowering time respectively (Kalih et al. 2014). Similarly, a co-localization for a QTL of FHB resistance and a QTL of plant height was observed on the chromosome 5R by Dhariwal et al. (2018). This QTL was reported to explain 23% of the phenotypic variance for FHB resistance and 13% of the phenotypic variance for plant height (Dhariwal et al. 2018), but the absence of common markers with this study does not allow to draw unambiguous conclusions about its identity with *Ddw1*.

Association of QTL for FHB resistance and plant height, focus on *Ddw1*

In this study, we investigated the association of plant height and FHB resistance with specific focus on the dwarfing gene *Ddw1*. The possibility to select for short plant types with high level of FHB resistance is indeed of high interest in cereal breeding. The frequently detected co-localization of QTL for both traits caused either by linkage or pleiotropy may render the achievement of this breeding goal a difficult task (Buerstmayr et al. 2012; Miedaner & Longin 2014; Prat et al. 2017; Talas et al. 2011). In this study, the level of correlation between plant height and FHB resistance was larger than r=0.5 in the AG population only, which was mainly caused by the effect of *Ddw1*. Given that these two traits were not correlated in the T and E populations, many genotypes matching the breeding goal of high FHB resistance and medium to short stature were found in these two populations (Fig. 1) confirming previous results by Galiano-Carneiro et al. (2019). On the other hand, there was only one short-straw genotype showing high level of resistance associated in the AG population. These results confirm the observations of Kalih et al. (2014) who showed that large population sizes were necessary to identify rare short-straw genotypes due to the dwarfing allele of *Ddw1* with an acceptably high level of FHB resistance.

Introgressing wheat resistance factors in elite triticale, a promising path for enhancing FHB resistance of triticale

Crossing hexaploid triticale with hexaploid wheat, and backcrossing to triticale has been extensively used in the triticale breeding history and tends to produce natural hexaploid triticale with frequent translocations observed from the D genome towards the R genome (Jenkins 1969; Kiss 1966; Lukaszewski & Gustafson 1983; Merker 1975; Sanchez-Monge 1958). With 7 resistance alleles on the 9 QTL detected, including those of the 4 major effects QTL, the line G8.06 harbors a very promising QTL

combination. The digital phenotyping methods used in this study enabled a characterization of type 4 resistance. Whether the FHB resistance observed in the field was due mainly to type 1 or type 2 resistance warrants further investigations. Although both major wheat resistance factors from the ancestral bread wheat line CM-82036, *Qfhs.ifa-5A* and *Fhb1*, (Buerstmayr et al. 2003) were polymorphic in the three tested populations, no significant effect was found for *Qfhs.ifa-5A.* Steiner et al. (2019) discovered that *Qfhs.ifa-5A* improves resistance to initial infection most likely through a passive resistance mechanism by enhancing anther extrusion in wheat. The very high extent of anther extrusion typical for triticale may therefore mask the effect of this QTL. By contrast, the use of three related populations has allowed for the first time the detection and the validation of *Fhb1* in triticale. The recent genome wide association study performed on a panel of 133 diverse winter triticale cultivars and elite breeding lines by Galiano-Carneiro et al. (2019) did not disclose any FHB resistance QTL on the chromosome 3B. This possibly shows that *Fhb1* was absent in the triticale genepool and that the novel germplasm developed for our study is the first triticale breeding material with *Fhb1* introgressed.

Whitened kernel surface (WKS), a novel digital trait for scoring FHB resistance

Due to the complexity of resistance phenomena, the genetic architecture of resistance may vary depending of the specificities of the phenotyping method used for its evaluation. In this study, FHB resistance was evaluated for two FHB related traits. The first one assessed FHB symptom severity on a whole plot basis in the field (AUDPC) which encompasses an integrated measure for FHB severity but does not distinguish types of resistance in the sense of Schroeder and Christensen (1963). The second one was based on severity of symptoms on grains measured by WKS which is a measure for resistance to kernel infection, also called type 4 in the sense of Mesterházy (1995). Notably, similar genetic architecture of the resistance was observed for both traits, AUDPC and WKS, in the three tested populations. The four QTL with major effect on resistance to FHB were detectable with both the traditional field severity evaluation (AUDPC) as well as WKS. Similar LOD values were observed for *Fhb1*, *Ddw1*, and the QTL on the chromosome 7A for both traits. Higher heritability coefficients were found for WKS compared to AUDPC. WKS scoring

allows measuring symptoms on many samples in an easier way than field scoring, and Ollier et al. (2018) showed that WKS displays high correlations with the mycotoxin content.

Perspective for triticale breeding and conclusions

One of the main outcomes of this project was the detection and the validation for the first time, of *Fhb1* in a triticale background, which represents a significant step forward in improving FHB resistance for this crop. Surprisingly, despite a high effect on resistance, *Fhb1* has not yet been deployed in commercial small-grain cereal cultivars by European breeders (Steiner et al. 2017). The agronomic features of Sumai-3 and CM-82036, that are very far from high-yielding elite breeding germplasms, may be one of the main issues which hampered this introgression. The two steps of backcrossing with Santop, and the successive crosses with triticale elite cultivars that were realized in this study, enabled the development of novel FHB-resistant genotypes that are agronomically closer to modern European germplasm. These genotypes represent improved germplasm for continuing a pre-breeding process targeting an introgression of *Fhb1* in elite winter triticale cultivars. As an example, nine triticale lines with beneficial QTL combinations for FHB-resistance and very high level of resistance for both traits, AUDPC and WKS, have been identified, and appear attractive for future research and pre-breeding purposes (Online resource 9). They represent excellent candidates for enhancing FHB resistance in practical triticale breeding programs, and with seven resistant alleles on nine QTL detected, the breeding line and common parent of our population, G8.06, represents by itself a valuable genetic resource for triticale breeding.

Aside from *Fhb1* three further QTL on chromosomes 7A, 2B and 5R all with major effect on FHB resistance, were detected. The difficulty to identify markers in segregation with the QTL detected on chromosome 7A possibly restrains the use of this QTL in a breeding program despite its high effect on resistance. On the contrary, the QTL on chromosome 2B appears particularly interesting for marker assisted breeding and gene cloning. It was mapped with a much greater precision than the QTL on chromosome 7A and localized in a marker rich area, which enable the identification of diagnostic markers associated with the QTL. However, this original resistance factor with major effect on the FHB resistance still needs to be validated in different breeding material.

Regarding the use of the dwarfing gene *Ddw1* on the chromosome 5R in triticale breeding programs, wheat breeders used to select first for lines with dwarfing alleles, in particular *Rht* genes, and then compensate their negative effect on FHB resistance by pyramiding other resistance QTL (Lu et al. 2011; Prat et al. 2017). This strategy is appropriate, knowing that *Rht* genes have a positive impact on yield, whereas Alheit et al. (2011) concluded that the dwarfing gene *Ddw1* reduced grain yield in triticale. Hence, it may be more advantageous for triticale breeders to conserve the tall allele of *Ddw1* in their breeding lines and reduce the impact on stature by using other plant height QTL which do not have an impact on the resistance as for example the QTL we have identified on the chromosome 5A.

Those four QTL with major effect on the resistance to FHB, constitute promising candidates for improving resistance in triticale. The strong population effect characterized for *Fhb1* is a frequent feature for FHB resistance QTL (Pumphrey et al. 2007) and may be explained by numerous additional QTL with minor effects and interactions with the genetic background. By taking into account the entire genome with both, QTL with minor and major effect on resistance, genomic selection may be a useful strategy for FHB resistance breeding, rather than simple markers-assisted selection (MAS) based on few QTL with major effect only. Some preliminary results are available and appear promising (Arruda et al. 2015, 2016; Galiano-Carneiro et al. 2019; Steiner et al. 2017; Würschum et al. 2017), but other publications have concluded that genomic selection only slightly improved predictive ability compared to markers-assisted selection (Miedaner et al. 2017) or even led to lower accuracies than using QTL targeted markers alone (Rutkoski et al. 2012). Even so, marker-assisted selection has already demonstrated its efficiency for improving FHB resistance in wheat (Anderson et al. 2007; Miedaner et al. 2006; Salameh et al. 2011; Wilde et al. 2007), and could therefore be a more affordable option for triticale breeding programs in which high-density fingerprinting is not commonly implemented. Finally, the new scoring method based on digital evaluation of the whitened kernel surface (WKS) appears as an efficient and flexible tool to enable FHB resistance scoring and a large-scale identification of breeding lines with low risk of mycotoxin contamination.

TABLES

Table 1: Means of parents and mean, minimum and maximum values of populations, least significant differences at $\alpha < 0.05$ ($LSD_{0.05}$) and broad-sense heritability coefficient (H^2) or repeatability of analyzed traits

	Parents					Population				
	G8.06	Tulus	Agostino	Grenado	El Paso	T				
						Mean	Min	Max	$LSD_{0.05}$	H^2
FHB severity in field (AUDPC)										
overall mean	202	429	267	602	220	280	153	495	113	0.73
2014	115	322	126	696	119	148	34	377	72	0.83[b]
2015	42	106	63	189	91	58	4	296	50	0.81[b]
2016	607	941	752	1247	570	781	341	1416	331	0.51[b]
2017	42	346	129	277	101	133	17	623	117	0.82[b]
FHB severity on grain (WKS)										
overall mean	2.71	4.43	3.06	5.22	2.79	3.10	1.32	7.13	1.09	0.87
2014	2.49	6.16	3.36	4.59	1.81	3.33	0.86	8.93	1.43	0.97[b]
2015	2.64	3.9	2.30	5.26	2.93	2.81	1.02	9.25	1.04	0.95[b]
2017	2.99	3.3	3.51	5.80	3.62	3.15	1.07	8.53	1.12	0.96[b]
Flowering date[a]	29.8	29.5	29.3	30.5	29.5	29.9	27.4	31.6	1.1	0.86
Plant height (cm)	127	112	102	93	112	121	109	134	6	0.88

	AG					E				
	Mean	Min	Max	$LSD_{0.05}$	H^2	Mean	Min	Max	$LSD_{0.05}$	H^2
FHB severity in field (AUDPC)										
overall mean	303	130	584	116	0.77	216	98	450	90	0.74
2014	186	43	498	90	0.88[b]	157	52	745	118	0.50[b]
2015	74	8	235	78	0.43[b]	82	4	517	81	0.68[b]
2016	840	252	1612	302	0.67[b]	537	153	1193	243	0.60[b]
2017	113	6	407	71	0.88[b]	86	10	333	65	0.80[b]
FHB severity on grain (WKS)										
overall mean	3.04	1.57	5.59	0.85	0.89	2.98	1.69	6.69	0.71	0.86
2014	2.95	1.10	5.64	1.14	0.92[b]	2.88	1.29	8.12	0.92	0.96[b]
2015	2.88	0.81	7.63	1.26	0.94[b]	2.64	1.28	6.32	0.82	0.94[b]
2017	3.28	1.17	8.10	0.91	0.98[b]	3.41	1.53	7.34	0.98	0.94[b]
Flowering date[a]	29.4	27.9	31.8	1.1	0.56	29.6	27.5	31.5	1	0.83
Plant height (cm)	122	90	147	7	0.97	119	100	146	5	0.93

[a] Number of days from May 1st to anthesis

[b] Repeatability, means based on two replications

Table 2: Pearson correlation coefficients between FHB severity in field (AUDPC), FHB severity on grain (WKS), plant height (PH) and flowering date (Days after May 1st) for the overall means

	WKS			Plant Height			Flowering Date		
Population	T	AG	E	T	AG	E	T	AGp	E
AUDPC	0.78 ***	0.75 ***	0.61 ***	-0.10 n.s	-0.67 ***	-0.48 ***	0.08 n.s	0.23 *	-0.14 n.s
WKS				-0.25 *	-0.59 ***	-0.14 n.s	0.04 n.s	0.39 ***	-0.20 n.s
Plant height							0.25 **	-0.32 **	0.10 n.s

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
n.s non significant

Table 3: Locations and estimates of QTL for plant height (cm) and flowering date (days after May 1st) on the cross specific maps using cross specific models run with the *R/QTL* package

Population	chr	Pos (cM)	Closest marker	Add[a]	%PV[b]	LOD[c]	Range[d]
			Plant height				
AG	2B	113	*8535079*	-2.1	5.0	11.2	150.0
T	5A	100	*4211970|F|0-17:G>C-17:G>C*	2.5	16.5	5.0	28.0
AG	5A	15	*3615965*	4.5	3.8	9.1	12.0
E	5A	292	*4559414*	2.8	29.8	8.3	12.0
E	5B	188	*4369389|F|0-6:G>A-6:G>A*	0.4	27.4	7.8	31.3
E	5A x 5B	-	-	-	11.5	3.7	-
AG	5R	19	*Xiac129*	14.2	77.7	50.6	8.0
AG	5R x 2B	-	-	-	1.5	4.1	-
T	6A	103	*4339927|F|0-26:G>T-26:G>T*	3.3	28.7	8.0	11.3
			Flowering date				
AG	3A	17	*10503667*	-0.32	12.4	4.5	91.0
T	4A	12	*8531145|F|0-12:G>A-12:G>A*	-0.48	9.9	4.1	24.0
E	4A	146	*10514293*	-0.46	11.4	3.9	34.0
T	5R	568	*3613461|F|0-15:T>C-15:T>C*	-0.52	7.2	3.0	12.0
AG	5R	19	*Xiac129*	-0.49	24.5	8.1	9.0
E	6B	196	*8512302|F|0-65:T>C-65:T>C*	-0.41	13.7	4.6	55.0
E	7A	281	*4210643|F|0-29:A>G-29:A>G*	0.37	15	5.0	110.0

[a] Positive additive effects denote trait-increasing effect of the G8.06 allele; additive effects were estimated as half the difference between phenotype averages for the homozygotes

[b] Percentage of phenotypic variance explained by the QTL

[c] LOD (logarithm of the odds) above LOD threshold at the 0.05 level of probability obtained through a 1000-iteration permutation test

[d] Range of the confidence interval position for the QTL

Table 4: Locations and estimates of QTL for plant height (cm) on the consensus map, including chromosomes 2B, 3B, 5A, 5R, 7A, and using a parental model run on all the lines from the three mapping populations with the *mppR* package.

Chr	Closest marker	%PV[a]	LOD[b]	Pos[c]	Range[d]	Parent	Effect	T-test[e]
5R	*Xiac129*	53.3	36.0	79.4	7.9	Tulus	-0.5	n.s
						F1(Agos´xGren´)	-14.1	***
						ElPaso	0.1	n.s
5A	*3622789|F|0-8:G>A-8:G>A*	1.9	3.3	71.9	66.5	Tulus	0.2	n.s
						F1(Agos´xGren´)	-1.7	n.s
						ElPaso	5.4	***
5A	*4211970|F|0-17:G>C-17:G>C*	1.4	4.4	106.3	29.6	Tulus	-1.9	*
						F1(Agos´xGren´)	-0.9	n.s
						ElPaso	-2.1	**
5A	*3619312|F|0-12:G>C-12:G>C*	3.0	5.5	164.2	6.9	Tulus	-1.6	.
						F1(Agos´xGren´)	-3.6	***
						ElPaso	-0.9	n.s

[a] Percentage of phenotypic variance explained by the QTL

[b] LOD (logarithm of the odds) above LOD threshold at the 0.05 level of probability obtained through a 1000-iteration permutation test

[c] Best estimated position for the QTL in cM on the consensus Map.

[d] Range of the confidence interval position for the QTL

[e] Student's T-tests results indicating when the tested parental effect is significantly different from the effect of the shared parent.

. p < 0.10
* p < 0.05
** p<0.01
*** p< 0.001
n.s non significant

Table 5: Locations and estimates of QTL for FHB severity (AUDPC & WKS) on the cross specific maps using cross specific models run with the *R/QTL* package.

Trait	Population	chr	Pos (cM)	Closest marker	Add[a]	%PV[b]	LOD[c]	Range[d]	Validity per year
AUDPC	T	2B	58	*10517361|F|0-33:T>C-33:T>C*	43.40	26.2	12.5	33.6	All years
WKS	T	2B	58	*10517361|F|0-33:T>C-33:T>C*	0.60	14.5	7.2	32.0	2014, 2017
AUDPC	T	3B	78	*14479678|F|0-40:G>C-40:G>C*	38.09	21.7	10.8	32.1	All years
WKS	T	3B	78	*14479678|F|0-40:G>C-40:G>C*	0.60	29.7	12.7	52.0	All years
AUDPC	AG	3B	39	*gwm533*	44.04	14.0	4.8	72.4	All years
WKS	AG	3B	39	*gwm533*	0.48	14.1	5.1	52.0	All years
AUDPC	AG	5R	19	*Xiac129*	50.42	27.6	8.5	14.0	All years
WKS	AG	5R	19	*Xiac129*	0.57	30.2	9.6	8.0	All years
AUDPC	T	6A	40	*3605407|F|0-32:G>A-32:G>A*	7.39	10.2	5.8	72.9	All years
AUDPC	T	2B x 6A	-	-	-	6.7	4.0	-	2016
WKS	T	6B	29.3	*3619611|F|0-12:A>G-12:A>G*	-0.19	7.5	4	24.4	2015, 2017
AUDPC	E	6B	114	*4369576|F|0-15:G>T-15:G>T*	-23.09	14.9	3.8	136.0	All years
AUDPC	E	7A	198	*8514068*	24.64	18.9	4.7	12.0	All years
WKS	E	7A	198	*8514068*	0.33	19.6	4.4	26.0	All years
AUDPC	T	7B	16	*3043611|F|0-39:T>C-39:T>C*	31.09	16.3	8.6	80.0	All years
AUDPC	T	3B x 7B	-	-	-	12.2	6.8	-	All years
WKS	T	7B	16	*3043611|F|0-39:T>C-39:T>C*	0.32	8.3	4.4	82.0	2017
WKS	T	3B x 7B	-	-	-	7.2	3.9	-	2017

[a] Positive additive effects denote trait-increasing effect of the G8.06 allele; additive effects were estimated as half the difference between phenotype averages for the homozygotes

[b] Percentage of phenotypic variance explained by the QTL

[c] LOD (logarithm of the odds) above LOD threshold at the 0.05 level of probability obtained through a 1000-iteration permutation test

[d] Range of the confidence interval position for the QTL

Table 6: Locations and estimates of QTL for AUDPC on the consensus map, including chromosomes 2B, 3B, 5A, 5R, 7A, and using bi-allelic and parental models run on all the lines from the three mapping populations with the *mppR* package.

Chr	Model	Closest marker	%PV[a]	LOD[b]	Pos[c]	Range[d]	Parent	Effect	T-test[e]
2B	Parental	*10517361|F|0-33:T>C-33:T>C*	9.4	6.6	144	14.1	Tulus	38.6	***
							F1(Agos´xGren´)	-13.2	n.s
							ElPaso	-29.5	**
	Bi-allelic	*11911490|F|0-41:G>T-41:G>T*	10.5	6.9	149.7	1.3	Tulus	39.9	***
							F1(Agos´xGren´)	0.0	n.s
							ElPaso	0.0	n.s
3B	Parental	*10524243|F|0-32:G>A-32:G>A*	14.7	8.9	59.7	15.5	Tulus	44.8	***
							F1(Agos´xGren´)	30.9	***
							ElPaso	22.4	**
	Bi-allelic	*14479870|F|0-26:A>T-26:A>T*	9.7	7.6	67.4	20.9	Tulus	28.6	***
							F1(Agos´xGren´)	28.6	***
							ElPaso	28.6	***
5R	Parental	*Xiac129*	8.1	6.3	79.4	11.3	Tulus	5.3	n.s
							F1(Agos´xGren´)	52.8	***
							ElPaso	14.0	.
	Bi-allelic	-	-	-	-	-	-	-	-

[a] Percentage of phenotypic variance explained by the QTL

[b] LOD (logarithm of the odds) above LOD threshold at the 0.05 level of probability obtained through a 1000-iteration permutation test

[c] Best estimated position for the QTL in cM on the consensus Map.

[d] Range of the confidence interval position for the QTL

[e] Student's T-tests results indicating when the tested parental effect is significantly different from the effect of the shared parent.

. $p < 0.10$

* $p < 0.05$

** $p<0.01$

*** $p< 0.001$

n.s non significant

Table 7: Confirmation per cross validation of the QTL with major effect on the resistance presented in Table 6.

Chr	Model	Pos[a]	N[b]	p.Ts[c]	p.Vs[d]	Bias[e]
2B	Parental	144	63	9.4	6.5	0.3
	Bi-allelic	149.7	76	10.4	8.6	0.2
3B	Parental	59.7	96	14.4	10.7	0.3
	Bi-allelic	67.4	41	9.5	7.7	0.2
5R	Parental	83.3	47	9.0	5.1	0.4
	Bi-allelic	-	-	-	-	-

[a] Best estimated position for the QTL in cM on the consensus Map.

[b] Number of occurrences of the QTL apparition across the 100 repetitions

[c] Percentage of phenotypic variance explained by the QTL in the global training set gathering the training sets of each cross.

[d] Weighted average, accounting for the cross sizes, of the within cross values of the Squared Pearson correlation between the observed and predicted phenotype values in the validation set.

[e] Bias= 1 - (p.Vs/p.Ts), Measure of the relative difference between p.Ts and p.Vs. More the bias is close to 0 more the QTL is stable.

FIGURES

Figure 1 Scatter plots and marginal histograms of frequency distribution of BLUEs for: FHB severity on grains (WKS) against plant height (cm) for **(A)** the T population; **(B)** the AG population; **(C)** and the E population; and for FHB severity in field (AUDPC) again plant height (cm) for **(D)** the T population; **(E)** the AG population; **(F)** and the E population. Parents are indicated by arrows.

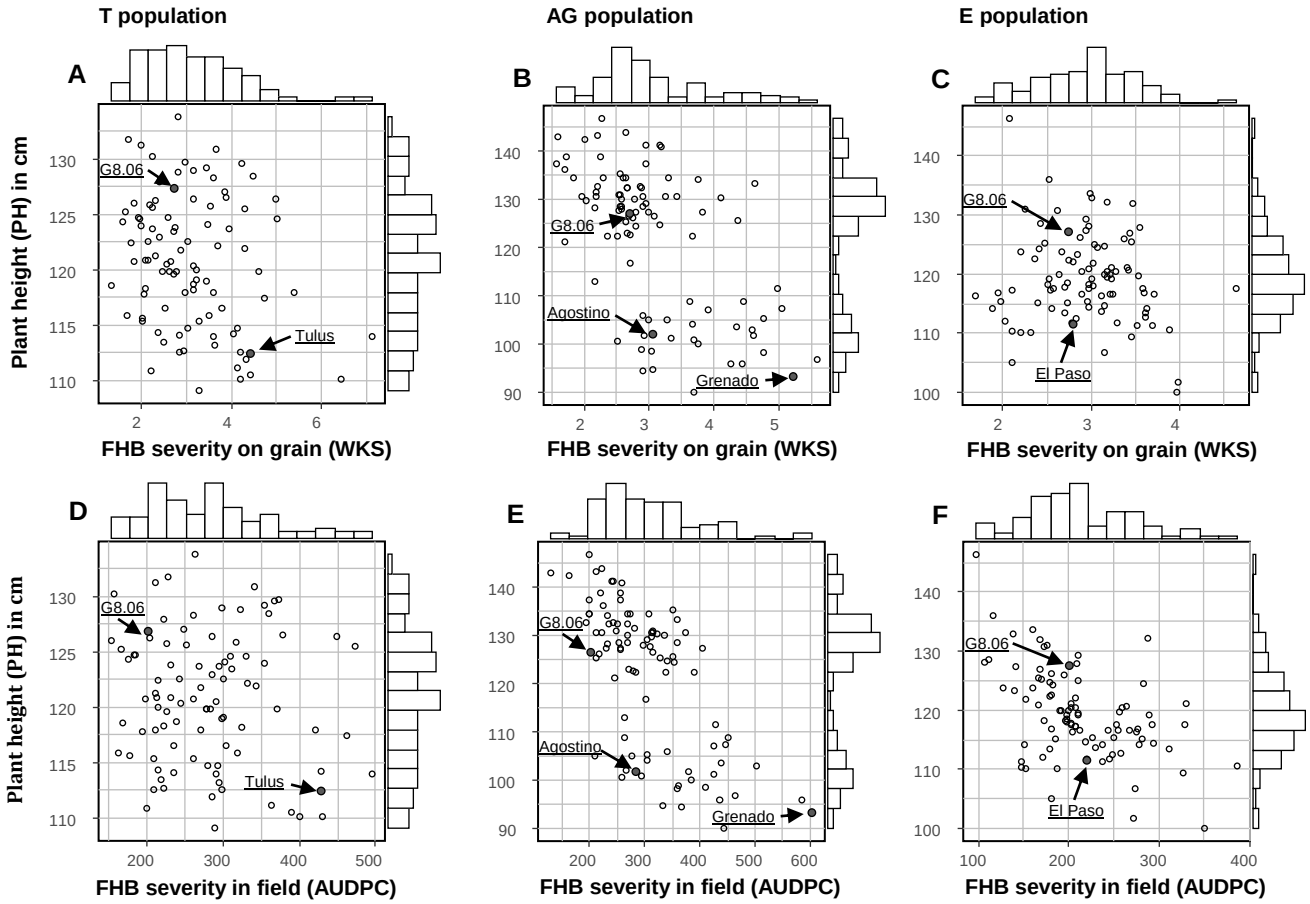


Figure 2 Box plot distributions of F_4 according to their alleles at *Fhb1* and *Qfhs.ifa-5A* loci for the three tested populations based on BLUEs of FHB severity on grain (WKS). BLUEs were calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations FHB severity on grain (WKS) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.

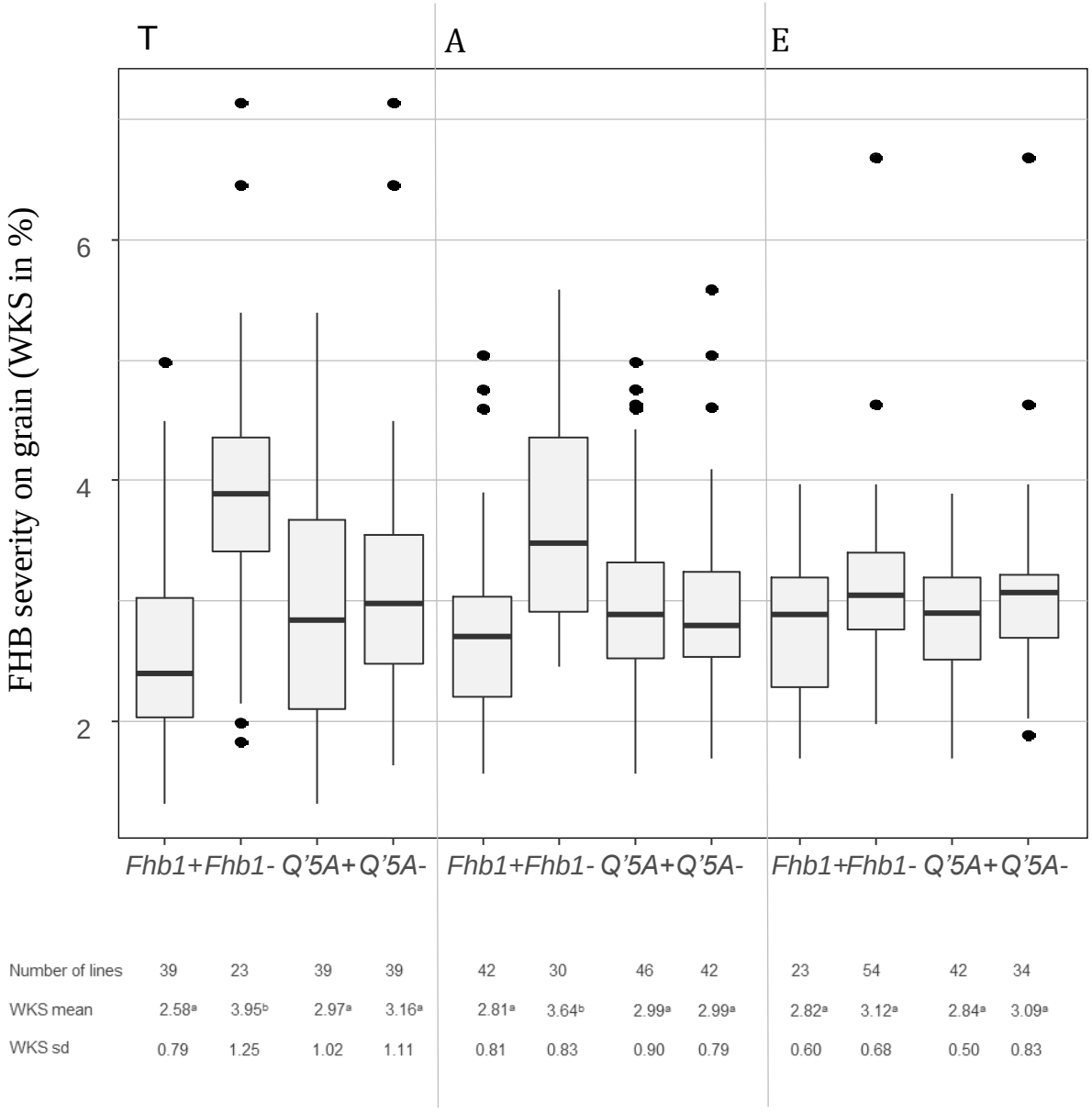
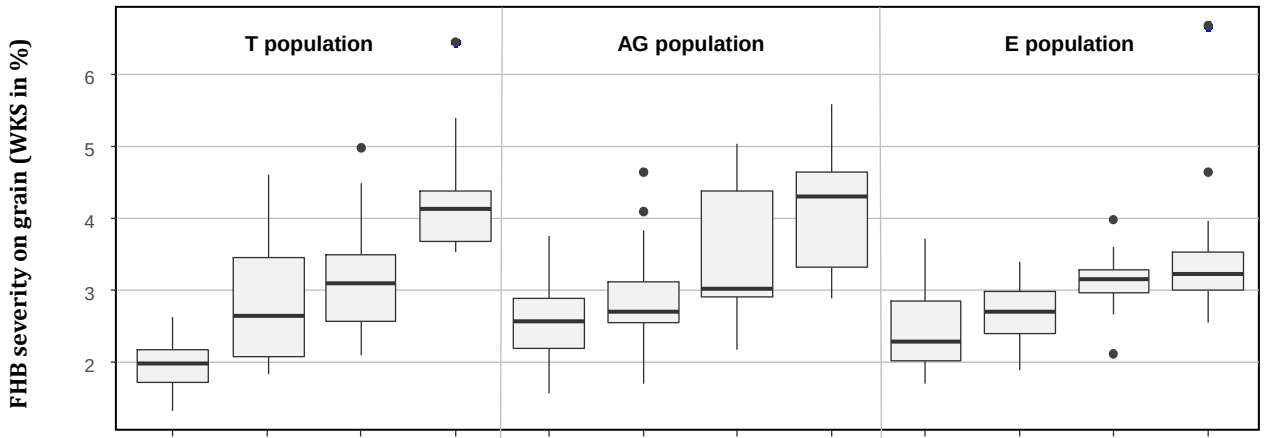


Figure 3 Box plot distributions of F_4 according to their allele combinations at the two main FHB resistance loci for each of the three populations based on BLUEs of FHB severity on grain (WKS) calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations of FHB severity on grains (WKS) and plant height (cm) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.



	2B+ Fhb1+	2B+ Fhb1-	2B- Fhb1+	2B- Fhb1-	ddw1-wt Fhb1+	ddw1-wt Fhb1-	Ddw1-mut Fhb1+	Ddw1-mut Fhb1-	7A+ Fhb1+	7A+ Fhb1-	7A- Fhb1+	7A- Fhb1-
Number of lines	14	7	16	10	32	31	10	16	8	25	10	36
WKS mean	1.96^{a}	2.88^{ab}	3.16^{c}	4.34^{c}	2.50^{a}	2.84^{ab}	3.47^{bc}	4.08^{c}	2.47^{a}	2.64^{a}	3.11^{ab}	3.37^{b}
WKS sd	0.32	0.94	0.82	0.88	0.51	0.59	0.95	0.82	0.62	0.40	0.48	0.69
Height mean	122^{a}	121^{a}	122^{a}	120^{a}	133^{a}	129^{a}	104^{b}	102^{b}	118^{a}	122^{a}	114^{a}	119^{a}
Height sd	5	6	6	7	5	6	5	8	6	8	7	7

ONLINE RESOURCE CAPTIONS

Online Resource 1 (ESM_1) Overview of the climatic conditions observed at IFA-Tulln (Austria) for the years 2014 to 2017, with the level of precipitation (mm) draw in solid line, and the average temperature (°C) draw in dashed line.

Online Resource 2 (ESM_2) Short Back up on the whitened kernel surface (WKS) method **(A)** Example of photo studio set-up; **(B)** Decision tree for sorting the pixels of the picture into background, healthy grains and whitened grain pixels. Extracted from Ollier et al. (2018); **(C)** AUDPC as a function of WKS for the three triticale populations with each dot representing a BLUE calculated across all experiments. WKS was calculated for a blue-level-limit of 150. Lm1, Lm2 and Lm3 illustrate linear regressions for the model AUDPC~WKS, with respective adjusted R-square of 0.61 ($p<0.0001$), 0.56 ($p<0.0001$), 0.37 ($p<0.0001$), for the T, AG and E populations.

Online Resource 3 (ESM_3) Variance component estimates of genotype $\sigma^2_{Genotype}$, year σ^2_{Year}, block within year $\sigma^2_{Block\ within\ Year}$, genotype × year $\sigma^2_{Genotype\ x\ Year}$ and the residual effects σ^2 error for FHB severity (AUDPC, WKS), plant height and flowering date across three experiments for populations T, AG, E.

Online Resource 4 (ESM_4) Linkage maps and positions of the four QTL with major effect on FHB severity and coinciding morphological traits in the three populations based on BLUEs calculated across all experiments. For readability, only selected markers are shown. Loci closest to the QTL peak of FHB severity are in bold. QTL bars span an LOD drop of 1.5 from maximum LOD.

Online Resource 5 (ESM_5) Chromosome locations and positions of markers in cross-specific and consensus linkage maps of the T, AG and E populations.

Online Resource 6 (ESM_6) Box plot distributions of F_4 according to their alleles at *Fhb1* and *Qfhs.ifa-5A* loci for the three tested populations based on BLUEs of FHB severity in field (AUDPC). BLUEs were calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations of FHB severity

in field (AUDPC) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.

Online Resource 7 (ESM_7) Additional information regarding the FHB resistance QTL detected on chromosome 2B, with **(A)** the blasting information of the markers present in the confidence interval of the QTL, and **(B)** the functional annotation of the 48 high confidence genes present in the confidence interval of the QTL

Online Resource 8 (ESM_8) Box plot distributions of F_4 according to their allele combinations at the two main FHB resistance loci for each of the three populations based on BLUEs of FHB severity in field (AUDPC) calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations of FHB severity in field (AUDPC) and plant height (cm) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.

Online Resource 9 (ESM_9) Promising FHB resistant lines with their allelic composition for the 4 QTL with major effect on the FHB resistance mapped on chromosome 3B, 5R, 2B and 7A, and complementary phenotyping information on their plant height and FHB resistance level.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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GENERAL DISCUSSION

Mycotoxins contamination is today a major concern in food and feed safety. Growing Fusarium head blight (FHB) resistant cultivars are of foremost importance for crops such as triticale, which are used mostly on the farm where they are produced, as animal feed, without checking for a potential mycotoxins risk contamination. However, relatively little research has been conducted to understand the bases of FHB resistance in triticale and elucidating its genetic architecture (Dhariwal et al., 2018; Galiano-Carneiro et al., 2018; Kalih et al., 2014, 2015; Miedaner et al., 2016) whereas bases of genetic resistance in bread wheat are now well described. Hexaploid wheat and triticale are closed relatives and share two of their three genomes, A/B/D and A/B/R for hexaploid wheat and triticale, respectively. As most of the QTLs described for wheat are located on the A and B genomes (Buerstmayr et al., 2009; Liu et al., 2009; Löffler et al., 2009), bread wheat represents a useful reservoir of resistance factors for triticale. The objectives of this thesis were thus to develop digital measurements for FHB symptoms, to get further insight into the genetic architecture of FHB resistance in triticale, to examine the effect of two well characterized bread wheat resistance factors, *Fhb1* and *Qfhs.ifa-5A,* in triticale genetic backgrounds, and to show the breeding value of introgressing wheat factors in elite triticale germplasms. The presence in one of our populations of both alleles of the gene *Ddw1*, the dwarfing and the wild ones, allowed us to investigate the association of plant height and FHB resistance with specific focus on the effect of this dwarfing gene.

Assessing Whitened Kernel Surface by digital picture analysis:

A competitive alternative to FDK for scoring FHB type IV resistance in cereals

The evolutions of the genotyping tools (i.e., from few descriptive markers to high-throughput and low-cost genotyping platforms and full sequence information) have made phenotyping a limiting factor for genetic gain increase in breeding in cultivated species. Identification of resistant breeding lines and factors relies on the availability of methods for assessing the trait of interest in a reproducible and reliable manner. This scoring step use to be costly in term of time and human resource and tools for high-throughput and low-cost measurement are therefore of foremost importance for enhancing selection efficiency. In order to assess FHB symptom severity, breeders rely on visual scoring on spikes in the field or estimate visually the proportion of Fusarium-damaged kernels (FDK) on harvested grain samples. Both scoring methods are time and labor intensive. Moreover, they require skilled assessors and can be subjective and assessor-dependent. For triticale, the natural grey hue of the kernels partially masks the apparition of FHB-symptoms and makes the visual screening particularly laborious compare to wheat. Digital image analysis is therefore a promising alternative to efficiently and accurately assess FHB severity.

Through this thesis we developed a new approach to quantify FHB severity on grains by the digital estimation of the whitened kernel surface (WKS). FHB diseased kernels tend indeed to appear smaller, shriveled and show white to pale pink discoloration (Abramson et al., 1987; Á. Mesterházy et al., 2005; Ruckenbauer et al., 2001). Based on a RGB analysis, the assessment of WKS can easily be implemented into a computer algorithm in Python or in other programming languages such as JAVA or C++. Tested on bread wheat and triticale, WKS appears as a reliable tool to quantify FHB severity on infected grain samples in comparison to other measurements such as field scoring, FDK or DON content. The coefficients of correlation between WKS-FDK and WKS-DON found in the two sets of bread wheat kernels were in a similar range as those reported for other optical methods such as hyperspectral imaging (Jayme G A Barbedo et al., 2015), near-infrared spectroscopic (NIR) measurement (Jin et al., 2014; Peiris et al., 2010), or RGB analyses (Maloney et al., 2014).

WKS is calculated as the percentage of whitened grain pixels among all grain pixels. To evaluate this proportion, the pixels in each picture are segregated into three categories, blue background, healthy grain and whitened grain. This segregation is based on their respective levels of red, green and blue. Pixels with a major red component are counted as grain pixels and others are classified as background pixels. Among grain pixels, distinction between healthy and whitened ones is based on their respective level of blue. An increase of the blue-level in a grain pixel is indeed an indication of whitening. We showed a blue-level-limit of 140 appropriate to distinguish pixels representing Fusarium damaged grain area from healthy grain area in two sample sets of wheat and one of triticale. However, three sample sets of kernels are not a sufficiently large basis for setting this blue-level-limit as a universal standard, and re-calibration to obtain an appropriate blue-level-limit is highly recommended. We suspect indeed a major effect of the photo studio settings on this optimal blue-level value, which might also depend on the specific grain samples under investigation, on the lamp or on the camera features. One of the main difficulty we faced to evaluate WKS on a reproducible manner, was the standardization of the photo tacking conditions. Thanks to a partnership with INRA, UMR GDEC, we discovered that the use of a basic office scanner permitted to get standardized pictures in a much easier way than with the photo studio we presented in the publication. Outside this standardization difficulty, the variability in WKS for the same sample, either due to the assortment of the grains on the image or to the camera, remained high, allowing valuable sample ranking.

One potential problem related with kernel scoring arises when samples with different natural grain color must be evaluated. In the case of visual FDK evaluation, the assessor can intuitively recalibrate his/her visual notation to avoid attributing naturally light-colored kernels as Fusarium damaged. With WKS measurement, this potential problem may be avoided by carefully setting the blue-level-limit high enough in order not to count naturally light-colored kernels as infected. When the samples under evaluation display very large variation in natural grain color, allocating the samples into subsets is recommended in order to determine an appropriate blue-level-limit for each subset.

Shriveling and white to pale pink discoloration of grains are well known as typical symptoms of FHB infection, while WKS measurement rests on pixel-whitening only. This simplification in symptom

evaluation is only reliable for samples coming from inoculated experiments where kernel whitening is induced by Fusarium head blight infection. The high levels of correlation observed between WKS and FDK show that the assessment of kernel whitening is sufficient to quantify FHB severity on grain for infections caused by *Fusarium graminearum* and/or *F. culmorum*. WKS appears therefore as a suitable method to assess resistance to kernel infection, also termed type IV resistance (Mesterházy et al., 1999).

Due to the complexity of the resistance phenomena, the genetic architecture of resistance may vary depending of the specificities of the phenotyping method used for its evaluation. However, we characterized similar genetic architecture of the resistance for both traits, severity in field and WKS. The four QTL with major effect on the resistance to FHB identified during this thesis, were detectable with both measurements and heritabilities were higher for WKS than for the visual field scoring. Digital scoring of WKS on harvested grains samples allows measuring symptoms on many samples in an easier way than field scoring. Measuring WKS is indeed fast, requires only basic equipment and does not necessitate sophisticated training or expertise. The Measurement can be performed any time after harvesting, which give timing and labor management a lot of flexibility, and the automatization of the scoring process avoids the assessor effect as well as the subjectivity inherent to visual scorings. As a high-throughput and low-cost method, WKS should be considered in the future as a competitive alternative for quantifying FHB severity on a large-scale basis and breeding resistant cereal varieties.

Next evolutions for the digital evaluation of Fusarium head blight symptoms:
For the WKS scoring and beyond

The pixel sorting process presented in this thesis allows a reliable quantification of FHB symptoms on grains through the measurement of the whitened kernel surface (WKS). The method has been tested on bread wheat and triticale and could easily be extended to other cereal crops such as durum wheat, rye or barley.

With the present method, the evaluation of the whitening on grain pixels is simply based on a measure of the blue-level. The associations between red, green, blue levels, hue, intensity, and saturation for diseased and healthy grain pixels, deserve further examination. Machine learning tools may enhance the accuracy of the scoring by establishing more sophisticated segregation criteria to distinguish between healthy and diseased pixels. They could also in the future help identifying differences in FHB symptoms caused by *Fusarium spp* and *Microdochium nivale*. Cereals kernels highly infected by Fusarium head blight tend to be smaller and whiter than healthy ones. It has been demonstrated that these very small and very white kernels greatly contribute to the global DON content of a grain set (Snijders & Perkowski, 1990). When evaluating the whitened kernel surface, the importance of a kernel in the global score of the kernel set is proportional to its surface. A promising research path to further increase the WKS-DON correlation would be to calculate an adjusted WKS for which the diseased pixels would be sorted by whitening categories. Appropriate weights could be assign to each category, particularly for the very white pixels from small kernels heavily infected by DON. These more complex approaches have not been explored yet and could increase the value of the WKS scoring.

Even though WKS scoring is already high-throughput, a possibility to further simplify the scoring of FHB would be to perform the digital evaluation directly in field. By using drones, a scoring based on hyperspectral imagery could approximate the visual evaluation of the proportion of infected spikelets performed on a whole plot basis. However, correlation with mycotoxin content is better when the scoring is performed on grain rather than on spikelet (Paul et al., 2005, 2006). A promising solution to

evaluate symptoms on grain directly in the field would be to acquire the data on combine during the harvest as it is already done for other quality traits. The presence of straw wastes would not allow a precise scoring of the WKS, as this method is simply based on an RGB analysis. In this context NIR would probably be the best option with equations established to approximate either the FHB-symptoms on grain or the DON content.

Breeding for a low mycotoxin content though an external scoring:

WKS, a valuable tool to breed cereals that resist mycotoxin accumulation

Despite feasible, the measurement of toxin content is time consuming, costly and not routinely performed on high numbers of samples as typical for a breeding program. If an accurate prediction of DON content in samples based on indirect measures such as field scores (Paul et al., 2006), hyperspectral imaging (Barbedo, Tibola, & Lima, 2017) or WKS (Ollier et al., 2018) is unrealistic, ranking of samples for DON content using scorings of FHB severity on grain is highly meaningful. Artificially inoculated experiments usually reach higher disease severities on grains than those observed in conventional cereal production on farmer's fields. Cereals kernels tend to appear smaller, shriveled and show white to pale pink discoloration when highly infected by Fusarium head blight. Hence, in inoculated experiments, significant and positive correlations between visual symptoms and DON content have frequently been found (Buerstmayr & Lemmens, 2015; Lemmens et al., 2016; Paul et al., 2005, 2006). Plant breeders aim primarily at ranking their breeding lines to select the most promising ones from their breeding population, rather than measuring exact DON values. The relationship between Fusarium symptom severity on grain and DON content is influenced by environmental conditions (Paul et al., 2006), and the dominating Fusarium species or strains (Mesterházy et al. 2005). Therefore, the comparison of samples on Fusarium symptom severity on grain in the purpose of an indirect selection on DON content is only meaningful for samples coming from a same experimental trial. The comparable correlation coefficients between FDK-DON and WKS-DON we found suggest that digital WKS measurement is a competitive alternative to visual FDK scorings for indirect selection on mycotoxin content. A substantial gain in the targeted trait (reduced DON content) is indeed achievable by selecting for breeding lines with low WKS values. As an example, by selecting the best 20% of our bead wheat lines based on WKS values, we showed that the selected groups had on average 65% lower DON content compared to the means of the unselected sample sets. Evaluation of symptoms on grains using WKS, is therefore of high interest for breeding lines with lower risk mycotoxin contaminations.

QTL mapping for Fusarium head blight resistance:
Overview of the genetic architecture of the resistance in triticale

Three related mapping populations were analyzed through this thesis. Analyzing together these populations with large variation for FHB severity, allowed further dissecting the genetic basis of FHB resistance in different elite triticale genetic backgrounds, and jointly analyzed QTL detection and validation. QTL mapping was performed primarily with cross specific models in the three populations independently and was then completed with multi-parent population QTL mapping. The use of the parental model allowed comparing the effects of QTL detected in distinct cross-specific models and permitted a characterization of their instability in different genetic backgrounds. Whereas the bi-allelic model allowed a joint characterization of the QTL effects based on all available information across populations.

High broad sense heritabilities (i.e. >0.70) were estimated for FHB-severity traits, supporting the importance of genetic effects on FHB resistance. A total of 9 QTL with varying effect on FHB resistance were identified on chromosomes 2B, 3B, 5R, 6A, 6B, 7A, 7B confirming previous results about the quantitative inheritance of FHB resistance in triticale (Dhariwal et al., 2018; Kalih et al., 2015; Miedaner et al., 2016; Oettler, 2004). Among those QTL, only one was derived from the rye genome, and all resistant alleles except for the QTL on the 6B came from the common parent G8.06. Notwithstanding, significant transgressive segregation was observed in all populations, suggesting the presence of other resistance factors unable to map in our study. The relatively small population size with less than 100 individuals per population could limit the power of QTL detection with small effects. The building of a consensus map integrated markers of all chromosomes from our three mapping populations, would have allow to fully benefit of the increased power of detection of QTL mapping models for multi-parent population, and might have given a more precise characterization of the genetic architecture of the resistance in our three triticale populations. The consensus map for chromosomes 3B, 2B, 5A, 7A and 5R have been built. Although incomplete, this map has allowed a

more refine characterization of four QTL with major effect on the resistance to FHB mapped on chromosomes 3B, 2B, 7A and 5R.

Crossing hexaploid triticale with hexaploid wheat:

A valuable approach for taking advantage in triticale of advanced genetic research in wheat

Crossing hexaploid triticale with hexaploid wheat and backcrossing the F1 to hexaploid triticale have been extensively used in triticale breeding history and tends to produce natural hexaploid segregant triticale with frequent translocations observed from the D genome into the R genome (Jenkins, 1969; Kiss, 1966; Lukaszewski & Gustafson, 1983; Merker, 1975; Sanchez-Monge, 1958). No cytologic test has however been performed to check for the caryotype of G8.06 and confirm this assumption.

Our tentative for introgressing wheat resistance factors in elite triticale was positively reported for one QTL of the two targeted. Thus, even though both QTL, *Qfhs.ifa-5A* and *Fhb1*, were polymorphic in the three tested populations, no significant effect could be detected for *Qfhs.ifa-5A.* Steiner et al. (2019) showed recently that *Qfhs.ifa-5A* improves resistance to initial infection through a passive resistance mechanism by enhancing anther extrusion in wheat. The very high anther extrusion usually observed in triticale populations may therefore mask the effect of this QTL. However, further analyses will be needed to conclude rather this absence of effect is due to the specific impact of the three populations backgrounds or to a genetic specificity of triticale when compared to wheat. By contrast, and as mentioned above, the use of three related populations has allowed for the first time the detection and the validation of *Fhb1* into triticale. This significant step forward in improving FHB resistance for triticale is an additional reported example for the breeding benefits of crossing hexaploid triticale with hexaploid wheat. Regarding the exchange of resistance factors and the access to a broader diversity, both crop can benefit of such crossing. However, for triticale this breeding strategy is also a lever to make use of advanced genetic research in wheat.

Nine F_4 triticale lines with beneficial QTL combinations for FHB-resistance and very high level of resistance for both traits, FHB-severity in field and WKS, have been identified through this thesis research. These lines represent good candidates for enhancing FHB resistance into practical triticale breeding programs, and with eight resistant alleles on nine QTL detected, the common parent of our population, G8.06, represents by itself a valuable genetic resource for triticale breeding.

Improving Fusarium head blight resistance in triticale:
Focus on four QTL with major effect on the resistance

Four QTL with major effect on the resistance to FHB were detected on chromosomes 3B, 2B, 7A and 5R in our triticale populations. They constitute promising candidates for improving FHB-resistance in triticale.

Fhb1, a great candidate for breeding Fusarium head blight resistant triticale

One of the most promising marker-trait associations we found was the one identified on chromosome 3B and was mapped in the *Fhb1* interval between the SSR markers *GWM493* and *GWM533*. The effects of this QTL in our populations were in the same range than the one previously observed in bread and durum wheat (Buerstmayr et al., 2003; Prat et al., 2017). This first detection and validation of *Fhb1* in a triticale background marks a significant step forward in improving FHB resistance for this crop.

It is surprising that despite a high effect on the resistance and a well characterization, *Fhb1* has not been broadly introgressed in small-grain cereal cultivars by breeders. The agronomic features of Sumai-3 and CM-82036 that are very far from adapted elite breeding germplasms might be one of the main issues which hampered this introgression. The two steps of backcrossing with Santop, and the successive crosses with triticale elite cultivars that were realized for this PhD thesis, enabled the development of novel FHB-resistant genotypes that are agronomically closer to modern European germplasm. These genotypes are thus an encouraging base for starting a pre-breeding process targeting an introgression of *Fhb1* in elite triticale cultivars.

Ddw1, a dwarfing gene with interesting features for breeders

The QTL with major effect on FHB resistance identified on chromosome 5R was detected at the *Ddw1* position and was the only one overlapping with QTL for flowering date and plant height. Lines carrying the dwarfing allele of *Ddw1* were significantly more susceptible, considerably shorter and showed a delayed flowering time. A large effect of this QTL on plant height, and flowering time was previously described in rye and in triticale (Börner et al., 2000; Kalih et al., 2014), while an effect on FHB resistance was so far described in triticale only (Kalih et al. 2014). Wheat breeders used to select first for lines with dwarfing alleles, in particular *Rht* genes, and then compensate their negative effect on FHB resistance by pyramiding other resistance QTL (Lu et al., 2011; Prat et al., 2017). This strategy is of appropriate, knowing that *Rht* genes have positive impact on yield, whereas Alheit et al. (2011) concluded that the dwarfing gene *Ddw1* reduced grain yield in triticale. This assessment deserves further investigations in different environments and genetic backgrounds. However, if the negative influence on yield of *Ddw1* is confirmed, it may be more advantageous for triticale breeders to conserve the tall and FHB-resistant allele of *Ddw1* in their breeding lines and reduce the impact on stature by using other plant height QTL which do not have an impact on the resistance.

Fhb-7A, a powerful but thorny candidate for improving Fusarium head blight resistance

Aside from *Ddw1* an additional QTL with major effect on FHB resistance was detected on chromosomes 7A. In 2011, Jayatilake et al. reported a QTL on chromosome 7A from CS-Sumai 3-7ADSL with a high level of FHB resistance. Designated as *Fhb7AC*, this QTL mapped near the centromere and explained similar level of resistance than the QTL we detected on chromosome 7A. Further testing will be necessary to confirm if those two QTL are identical, but a potential proximity with the centromere could explain why the building of the consensus map around the QTL was so difficult with our three F_4 populations. The effect of the QTL we detected on the chromosome 7A, was significant in one population only. In this population, the closest marker we found in linkage disequilibrium with the QTL suggests that the common parent G8.06 would be the only parental line carrying the resistant allele for this QTL. This might be the sign of a very high population effect on the

QTL effect, however, the hypothesis of proximity between the centromere of the chromosome and the QTL could also explain this phenomenon. It could exist an important physical distance between the QTL and the marker with historical recombination events, which would have occurred in between for the lines Tulus, Agostino and Grenado. In this case, the parental line El Paso would be the only one really carrying the susceptible allele for this QTL, which would explain why the effect of the QTL is significant only in the Ep population. The integration of the marker *Xwmc17* into our maps and the generation of more lines for the Ep population in order to identified closer markers in linkage disequilibrium with the QTL will be necessary to validate this assumption. However, the difficulty to identify markers in segregation with the QTL detected on chromosome 7A could restrain the use of this QTL in a breeding program despite its important effect on the resistance.

Fhb-2B, a promising candidate for Fusarium head blight resistance breeding and gene-cloning

The third QTL detected in our mapping populations with a major effect on the resistance was mapped on the chromosome 2B. Several FHB resistance QTL with large effect have already been detected in bread wheat on this chromosome (Buerstmayr et al. 2009), but no reports have been found in the literature of any large effect QTL in chromosome 2B coming from populations with Sumai-3 in their pedigree. The QTL was polymorphic only in the T population, cross validation results performed with multi-parental models, showed comparable level of stability when comparing with *Fhb1*, and both QTL presented similar additive effects in the T population. As this QTL maps in a markers-rich area, it appears particularly interesting for enhancing FHB resistance in triticale. Further testing will be necessary to evaluate its stability in different genetic backgrounds or to refine its position in a purpose of cloning, but the present data are already promising.

Marker-assisted selection vs Genomic selection, which path for breeding resistant triticale?

Markers-assisted selection has already demonstrated its efficiency for improving FHB resistance in wheat (Anderson et al., 2007; Miedaner et al., 2006; Salameh et al., 2011; Wilde et al., 2007). The implementation of these four QTL in a native traits program relies on the availability of markers

closely linked with the QTL to characterize the germplasm. The closer the markers are, the more reliable the characterization will be. *Fhb1* and *Ddw1* have been broadly described by the past and are ready to be implemented. Few information is however available for the QTL we detected on chromosomes 2B and 7A. One of the advantages of the DartSeq platform used in this research is that it provides a large number of markers, increasing therefore the chance to have some of them physically close the QTL of interest. Additionally, it makes available the sequences of all its markers, which simplify the transfer toward genotyping platforms frequently used by breeding institutions, such as KASP or TaqMan. Although the case of the QTL we detected on the chromosome 7A remains problematic, the QTL we detected on chromosome 2B has been mapped in a reduced and markers-rich area. Further testing will be needed to validate the correlation between the markers in linkage disequilibrium with the QTL and the level of FHB-resistance. However, these markers constitute already promising candidates for the implementation of this QTL in markers-assisted selection (MAS) strategy.

In accordance with previous researches (Agostinelli et al., 2012; Balut et al., 2013; Buerstmayr et al., 2009; Prat et al., 2017; Pumphrey et al. , 2007; Verges et al., 2006), we showed that the effect of *Fhb1* on FHB resistance varied depending on the genetic background. This strong population effect is a frequent feature for FHB resistance QTL (Pumphrey et al. 2007) and could be explained by numerous additional QTL with minor effects and interactions with the genetic background. By taking into account the entire genome with both, QTL with minor & major effect on the resistance, genomic selection could be a better strategy for FHB resistance breeding than a simple markers-assisted selection (MAS) based on few QTL with major effect only. Some preliminary results are already available and seem promising (Arruda et al., 2015, 2016; Steiner et al., 2017; Würschum et al., 2017). The implementation of genomic selection for breeding FHB-resistant triticale relies however on the generalization of fingerprinting in triticale breeding programs. Despite the last reductions of the genotyping cost, such generalization is not yet expected, and a simple MAS strategy remains today a more affordable option.

CONCLUSIONS

This PhD project enabled the detection and the validation, for the first time in triticale backgrounds, of *Fhb1,* the most consistently reported QTL for FHB resistance in bread wheat. This significant step forward in improving FHB resistance for triticale is a new demonstration of the interest of crossing hexaploid triticale with hexaploid wheat to broaden diversity and to make use of advanced genetic research in wheat. Aside from *Fhb1*, three other QTL with major effect on the resistance to FHB were detected on chromosomes 2B, 7A and 5R and constitute promising candidates for improving FHB-resistance in triticale. The association of plant height and FHB resistance was significant in one population only, where polymorphism was detected for the gene *Ddw1*. Lines carrying the dwarfing allele of *Ddw1* were accordingly more susceptible, considerably shorter and showed a delayed flowering time. No significant effect could be detected for *Qfhs.ifa-5A,* the other introgressed QTL, probably due to specificity of triticale compare to wheat.

The new scoring method based on digital evaluation of the whitened kernel surface (WKS) appears as an efficient and flexible high-throughput tool to enable FHB resistance scoring and a large-scale identification of breeding lines with low risk of mycotoxin contamination and should therefore be considered as a competitive alternative for breeding highly FHB resistant cereal varieties in the future.

Nine F_4 triticale lines with beneficial QTL combinations for FHB-resistance and very high level of resistance for both traits, FHB-severity in field and WKS, have been identified through this thesis. These lines represent good candidates for enhancing FHB resistance and for reducing the risk of mycotoxin contamination into practical triticale breeding programs. G8.06, the common parent of our populations, represents also a valuable genetic resource for triticale breeding. It harbors indeed eight resistant alleles on the nine detected QTL.

Perspectives of improvements for the WKS method exist and should be explored in the future. The QTL we mapped on the chromosome 2B, deserves also further investigations as a promising candidate for breeding and for cloning purposes.

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APPENDICES

Publication 1 – Supplementary material

Figure S1. Example of the photo studio set-up for taking digital images of grain samples.

Figure S2. Digital images of ten samples from series BW1 displaying broad variation in Fusarium symptoms, with their respective WKS (whitened kernel surface), FDK (Fusarium damaged kernels), and DON (deoxynivalenol) content values. WKS was estimated applying a blue-level-limit of 140.

WKS (%): 3.44

FDK (%): 5

DON (ppm): 8.00

WKS (%): 4.58

FDK (%): 15

DON (ppm): 9.82

WKS (%): 5.40

FDK (%): 5

DON (ppm): 9.61

WKS (%): 7.95

FDK (%): 35

DON (ppm): 33.35

WKS (%): 11.16

FDK (%): 40

DON (ppm): 24.90

WKS (%): 15.47

FDK (%): 55

DON (ppm): 40.30

WKS (%): 15.63

FDK (%): 65

DON (ppm): 43.49

WKS (%): 17.23

FDK (%): 75

DON (ppm): 36.66

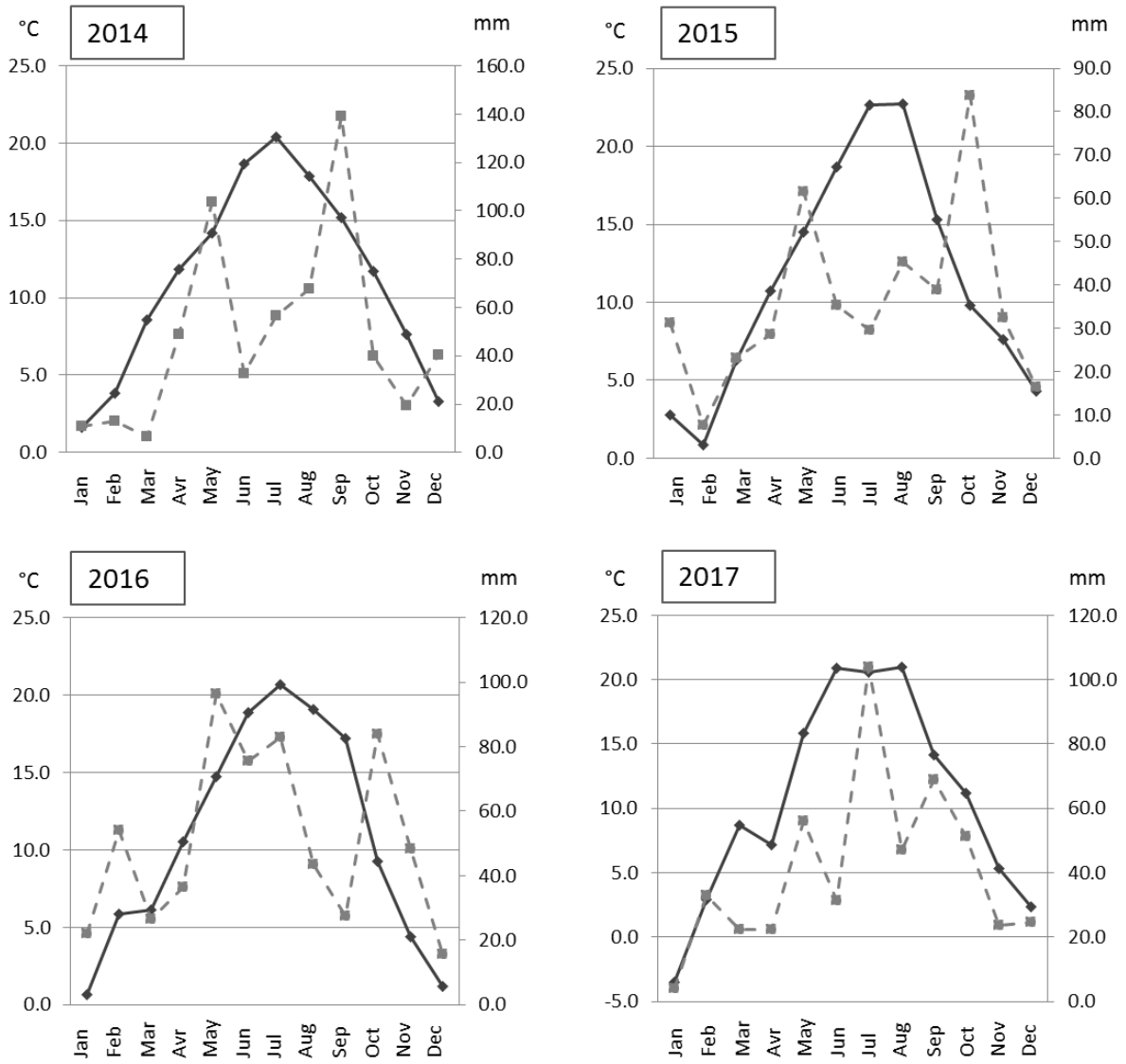
WKS (%): 20.91

FDK (%): 80

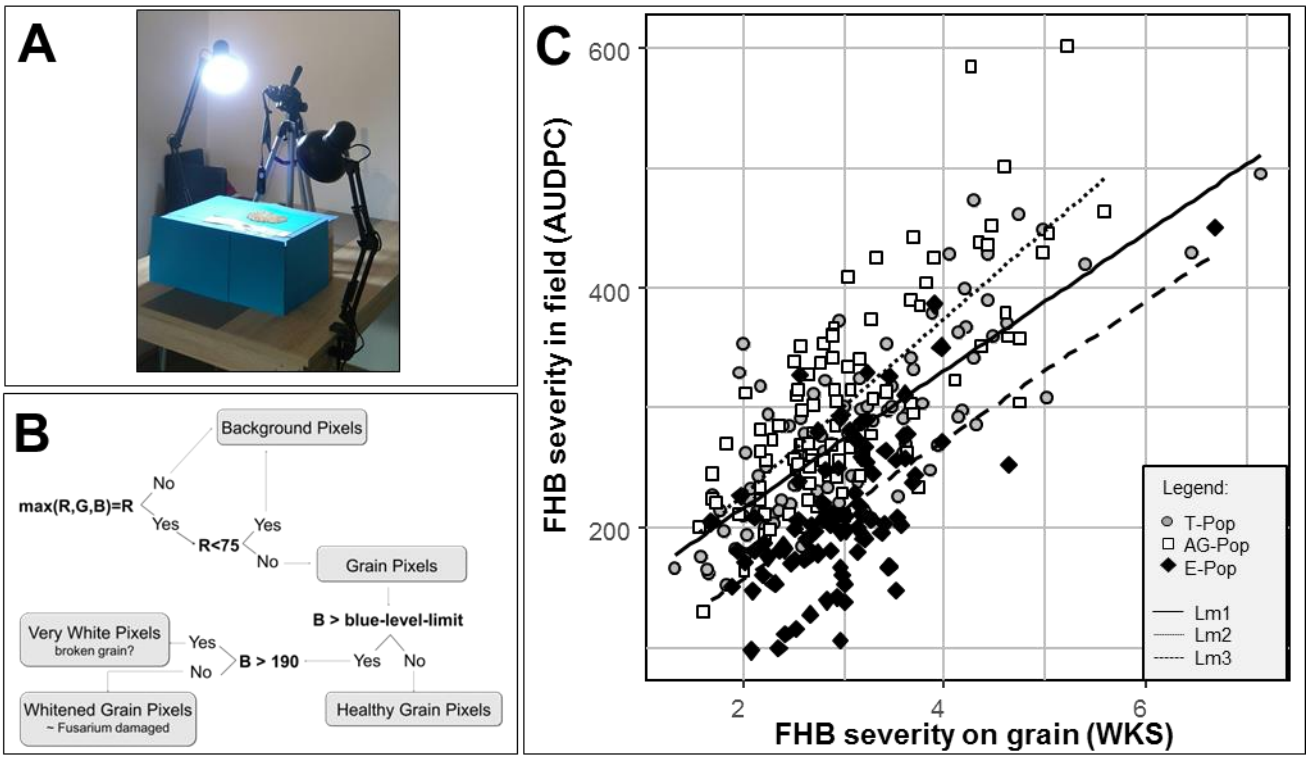
DON (ppm): 44.08

Publication 2 – Supplementary material

ESM_1 : Overview of the climatic conditions observed at IFA-Tulln (Austria) for the years 2014 to 2017, with the level of precipitation (mm) draw in dashed line, and the average temperature (°C) draw in solid line.



ESM_2 : Short Back up on the whitened kernel surface (WKS) method **(A)** Example of photo studio set-up; **(B)** Decision tree for sorting the pixels of the picture into background, healthy grains and whitened grain pixels. Extracted from Ollier et al. (2018); **(C)** AUDPC as a function of WKS for the three triticale populations with each dot representing a BLUE calculated across all experiments. WKS was calculated for a blue-level-limit of 150. Lm1, Lm2 and Lm3 illustrate linear regressions for the model AUDPC~WKS, with respective adjusted R-square of 0.61 ($p<0.0001$), 0.56 ($p<0.0001$), 0.37 ($p<0.0001$), for the T, AG and E populations.



ESM 3 : Variance component estimates of genotype σ2Genotype, year σ2Year, block within year σ2Block within Year, genotype × year σ2Genotype x Year and the residual effects σ2 error for FHB severity (AUDPC, WKS), plant height and flowering date across three experiments for populations T, AG, E

Tulus x G8.06 (T) population

Trait	Variance component				
	$\sigma^2_{Genotype}$	σ^2_{Year}	$\sigma^2_{Block\ within\ Year}$	$\sigma^2_{Genotype \times Year}$	σ^2_{error}
FHB severity (AUDPC)	4.41E+03	1.13E+05	9.17E+02	2.26E+03	8.39E+03
FHB severity (WKS)	9.79E-01	3.53E-07	1.40E-01	2.68E-01	3.68E-01
Plant height	3.17E+01	9.47E+01	1.09E+01	2.06E+00	2.87E+01
Flowering date	8.99E-01	6.54E+00	4.14E+00	4.10E-16	1.20E+00

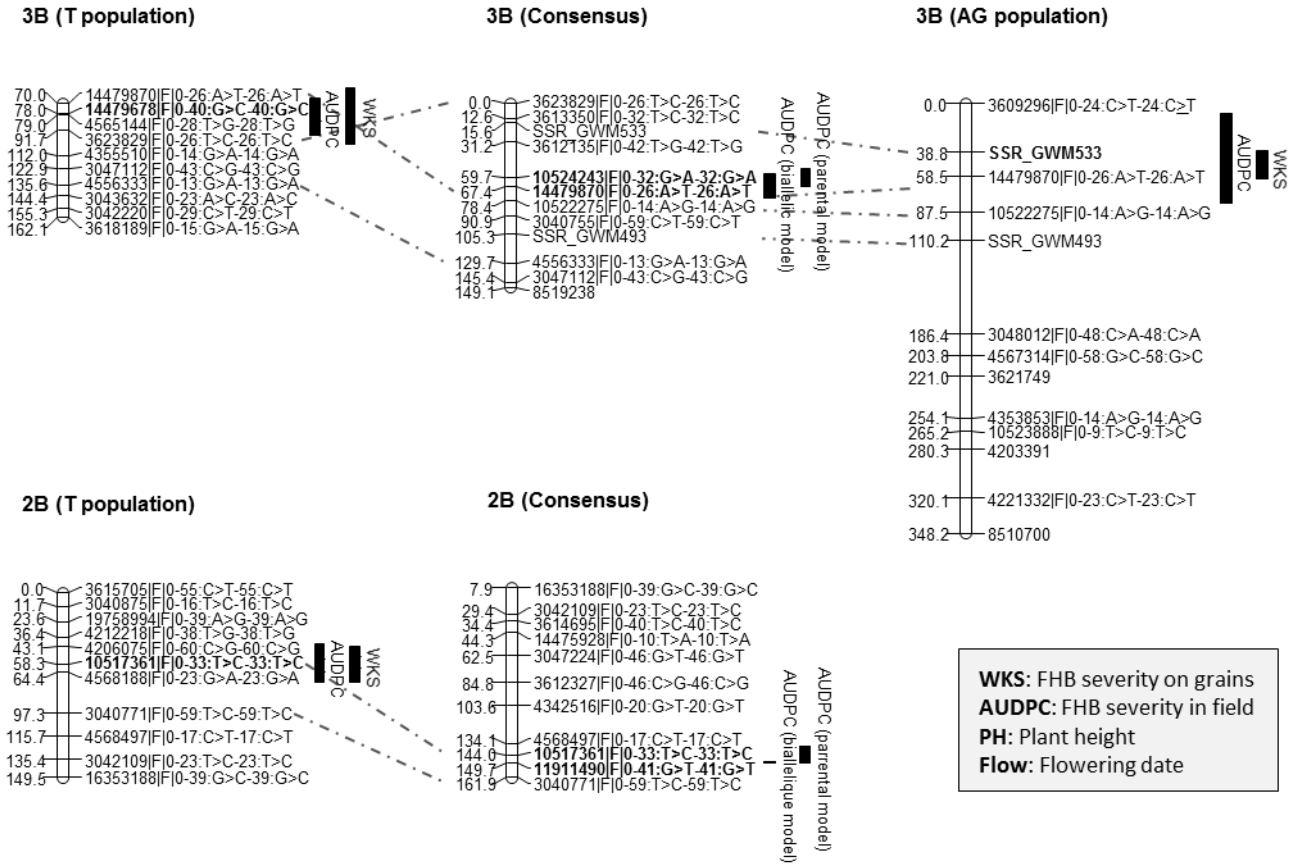
(Agostino x Grenado) x G8.06 (AG) population

Trait	Variance component				
	$\sigma^2_{Genotype}$	σ^2_{Year}	$\sigma^2_{Block\ within\ Year}$	$\sigma^2_{Genotype \times Year}$	σ^2_{error}
FHB severity (AUDPC)	5.77E+03	1.29E+05	3.11E+03	3.35E+03	7.02E+03
FHB severity (WKS)	6.93E-01	<1.0E-8	3.13E-01	1.08E-01	3.21E-01
Plant height	2.19E+02	9.62E+01	2.05E+01	1.68E+01	2.04E+01
Flowering date	5.76E-01	9.57E+00	1.69E+00	1.28E-01	9.87E-01

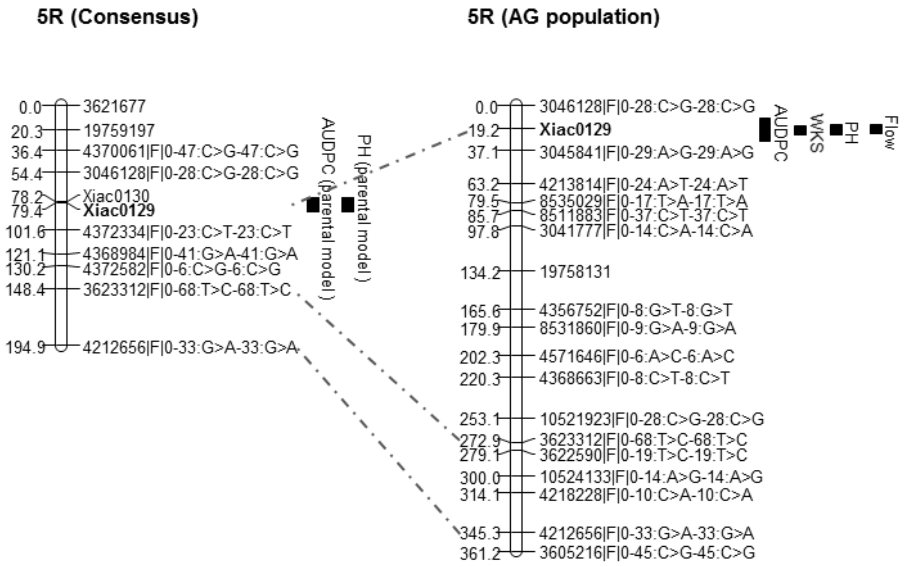
El Paso x G8.06 (E) population

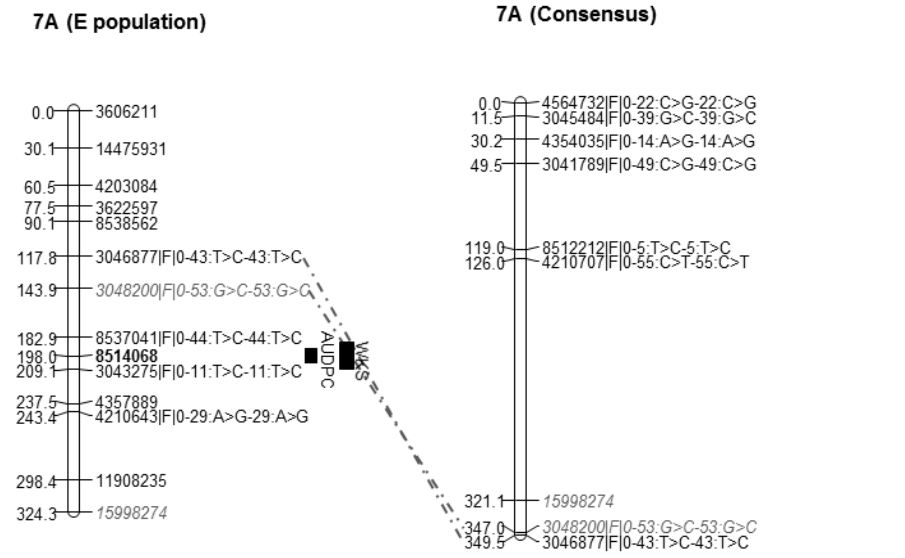
Trait	Variance component				
	$\sigma^2_{Genotype}$	σ^2_{Year}	$\sigma^2_{Block\ within\ Year}$	$\sigma^2_{Genotype \times Year}$	σ^2_{error}
FHB severity (AUDPC)	2.89E+03	4.47E+04	3.86E+03	1.41E+03	5.33E+03
FHB severity (WKS)	3.62E-01	8.92E-02	1.37E-01	7.21E-02	2.19E-01
Plant height	5.16E+01	8.34E+01	2.14E+01	1.25E+00	2.66E+01
Flowering date	6.26E-01	7.84E+00	1.97E+00	2.00E-10	1.11E+00

ESM_4 : Linkage maps and positions of the four QTL with major effect on FHB severity and coinciding morphological traits in the three populations based on BLUEs calculated across all experiments. For readability, only selected markers are shown. Loci closest to the QTL peak of FHB severity are in bold. QTL bars span an LOD drop of 1.5 from maximum LOD.



WKS: FHB severity on grains
AUDPC: FHB severity in field
PH: Plant height
Flow: Flowering date





ESM_5 : Chromosome locations and positions of markers in cross-specific and consensus linkage maps of the T, AG and E populations.

Tulus x G8.06 (T) population

Marker name	Linkage group	position (cM)
3045804|F|0-45:G>A-45:G>A	1A	0
3045804|F|0-47:T>C-47:T>C	1A	0
19759236|F|0-19:C>T-19:C>T	1A	2.4
4369261|F|0-8:A>G-8:A>G	1A	16.4
10517670|F|0-62:C>G-62:C>G	1A	22.5
3610194|F|0-25:C>T-25:C>T	1A	24.8
4367467|F|0-57:A>C-57:A>C	1A	27.5
3042676|F|0-43:T>C-43:T>C	1A	28.6
14475573|F|0-15:C>T-15:C>T	1A	29.4
4364222|F|0-25:A>T-25:A>T	1A	31.5
4201775|F|0-42:C>T-42:C>T	1A	32.9
4369015|F|0-64:G>A-64:G>A	1A	37.3
3041631|F|0-63:G>A-63:G>A	1A	38.6
4373231|F|0-40:A>G-40:A>G	1A	42.3
19758885|F|0-19:C>A-19:C>A	1A	44.3
4364504|F|0-18:G>A-18:G>A	1A	45.6
4220650|F|0-7:G>A-7:G>A	1A	48.8
4346304|F|0-6:G>A-6:G>A	1A	53.1
3048067|F|0-56:T>C-56:T>C	1A	54
3040686|F|0-18:C>T-18:C>T	1A	57.3
3044166|F|0-6:G>A-6:G>A	1A	69.4
4348093|F|0-56:G>A-56:G>A	1A	75.2
4202974|F|0-11:C>T-11:C>T	1A	75.2
4370789|F|0-12:T>C-12:T>C	1B	0
10523514|F|0-13:T>C-13:T>C	1B	0
3046820|F|0-32:A>G-32:A>G	1B	3.4
4367550|F|0-66:G>A-66:G>A	1B	6.7
10523287|F|0-10:G>C-10:G>C	1B	7.6
3614191|F|0-22:G>A-22:G>A	1B	12.1
4369022|F|0-37:G>C-37:G>C	1B	16.3
3042433|F|0-10:T>C-10:T>C	1B	17.8
4204453|F|0-17:A>G-17:A>G	1B	19.2
11911681|F|0-20:C>T-20:C>T	1B	22
4339730|F|0-16:C>T-16:C>T	1B	24.8
3603480|F|0-30:A>G-30:A>G	1B	27.8
3045316|F|0-48:C>A-48:C>A	1B	38.4
3618263|F|0-41:G>C-41:G>C	1B	39.7
3616740|F|0-43:A>G-43:A>G	1B	42.1
10516576|F|0-16:G>C-16:G>C	1B	42.9
4341077|F|0-22:C>G-22:C>G	1B	44

3048100|F|0-9:A>G-9:A>G	1B	46.4
3042917|F|0-48:C>G-48:C>G	1B	47.3
4553436|F|0-20:C>A-20:C>A	1B	47.9
3606717|F|0-37:G>C-37:G>C	1B	48.8
3616976|F|0-21:T>C-21:T>C	1B	49.5
3612566|F|0-41:A>T-41:A>T	1B	50.9
4368527|F|0-17:G>A-17:G>A	1B	52.8
3047799|F|0-55:C>T-55:C>T	1B	55.2
3044655|F|0-33:T>A-33:T>A	1B	58.4
3047834|F|0-34:C>T-34:C>T	1B	58.8
3045707|F|0-20:A>T-20:A>T	1B	61.2
3047419|F|0-44:A>C-44:A>C	1B	61.5
8510858|F|0-27:A>C-27:A>C	1B	63
3046044|F|0-56:C>A-56:C>A	1B	65
3617623|F|0-35:A>G-35:A>G	1B	68.2
3047035|F|0-37:C>G-37:C>G	1B	69.7
8512502|F|0-5:C>T-5:C>T	1B	70.7
3042037|F|0-66:C>T-66:C>T	1B	75
3041084|F|0-44:C>T-44:C>T	1B	76.6
16357573|F|0-25:A>C-25:A>C	1B	78.7
4211251|F|0-25:C>G-25:C>G	1B	79.6
3045148|F|0-31:G>A-31:G>A	1B	83.6
3047619|F|0-55:C>G-55:C>G	1B	84.9
3040656|F|0-58:G>A-58:G>A	1B	86.9
3617386|F|0-14:A>G-14:A>G	1B	88.4
3046404|F|0-43:C>G-43:C>G	1B	88.6
4345504|F|0-11:T>C-11:T>C	1B	90
3043781|F|0-13:G>A-13:G>A	1B	91.7
3040726|F|0-19:G>A-19:G>A	1B	92.3
3611442|F|0-25:G>T-25:G>T	1B	95.4
8509710|F|0-15:C>T-15:C>T	1B	96.6
8511549|F|0-49:C>A-49:C>A	1B	97.8
3605115|F|0-65:C>T-65:C>T	1B	98.3
3041239|F|0-21:A>G-21:A>G	1B	100.7
3041239|F|0-8:C>T-8:C>T	1B	100.7
3040598|F|0-36:A>G-36:A>G	1B	103.9
8511647|F|0-31:C>A-31:C>A	1B	107.2
3048108|F|0-24:C>G-24:C>G	1B	110
11910254|F|0-36:A>G-36:A>G	1B	112.6
8512765|F|0-25:G>T-25:G>T	1B	113.1
4358171|F|0-65:G>T-65:G>T	1B	115
3603731|F|0-15:G>C-15:G>C	1B	115.3
3043168|F|0-39:C>G-39:C>G	1B	121
3046904|F|0-42:C>T-42:C>T	1B	121.7
3041621|F|0-41:G>A-41:G>A	1B	123.2
3042199|F|0-56:T>A-56:T>A	1B	125.2
4371952|F|0-20:C>A-20:C>A	1B	130.6
8535241|F|0-29:A>T-29:A>T	1B	140.3

4346922|F|0-7:C>G-7:C>G	1B	143.3
4215445|F|0-23:G>A-23:G>A	1B	147.1
16356282|F|0-18:G>A-18:G>A	1B	149.8
3041802|F|0-20:C>T-20:C>T	1B	151.6
3618432|F|0-53:G>C-53:G>C	1B	153.5
3624373|F|0-9:G>C-9:G>C	1B	156.8
3611694|F|0-17:T>G-17:T>G	1B	160.2
11912125|F|0-15:C>T-15:C>T	1B	168.1
4372313|F|0-56:C>A-56:C>A	1B	170.7
3624634|F|0-44:A>G-44:A>G	1B	172.4
8511665|F|0-50:G>T-50:G>T	1B	172.5
3616825|F|0-37:T>G-37:T>G	1R	0
10516642|F|0-14:T>C-14:T>C	1R	0.2
8512333|F|0-9:G>C-9:G>C	1R	3.5
4215623|F|0-8:G>C-8:G>C	1R	6.1
4362749|F|0-28:G>C-28:G>C	1R	7.8
4370690|F|0-38:C>T-38:C>T	1R	9.9
4341637|F|0-6:T>C-6:T>C	1R	12.3
3621919|F|0-14:C>T-14:C>T	1R	13.8
10523462|F|0-10:T>C-10:T>C	1R	14.7
4358076|F|0-7:T>C-7:T>C	1R	16.4
4355769|F|0-11:T>C-11:T>C	1R	17.3
16312168|F|0-41:T>C-41:T>C	1R	18.4
3610710|F|0-18:C>A-18:C>A	1R	21.6
3046738|F|0-61:G>A-61:G>A	1R	24.5
10523762|F|0-16:A>C-16:A>C	1R	25.7
4373891|F|0-32:T>C-32:T>C	1R	27.1
3608318|F|0-16:G>C-16:G>C	1R	29
10519563|F|0-16:T>C-16:T>C	1R	29
4201394|F|0-10:T>C-10:T>C	1R	29.7
4209935|F|0-39:C>A-39:C>A	1R	30.8
4345030|F|0-9:G>A-9:G>A	1R	32.6
8538798|F|0-63:A>G-63:A>G	1R	33.3
4369310|F|0-6:C>G-6:C>G	1R	36.1
4202254|F|0-11:C>A-11:C>A	1R	36.1
3044713|F|0-49:T>C-49:T>C	2A	0
3043855|F|0-24:C>G-24:C>G	2A	0
3040551|F|0-19:T>A-19:T>A	2A	2
4565481|F|0-41:T>C-41:T>C	2A	5.5
3046836|F|0-36:C>T-36:C>T	2A	25
4207946|F|0-25:A>C-25:A>C	2A	27.7
3047120|F|0-7:A>G-7:A>G	2A	29.7
4207135|F|0-49:T>G-49:T>G	2A	31.1
4205323|F|0-24:G>A-24:G>A	2A	34
4213005|F|0-13:G>T-13:G>T	2A	36.4
8510173|F|0-5:A>C-5:A>C	2A	37.4
4343927|F|0-24:A>G-24:A>G	2A	40.3
4210030|F|0-24:G>C-24:G>C	2A	42.3

3046584|F|0-5:C>T-5:C>T	2A	44.4
3040864|F|0-68:T>C-68:T>C	2A	47.6
3047555|F|0-36:T>C-36:T>C	2A	50.2
4367426|F|0-67:C>T-67:C>T	2A	55.2
3047962|F|0-41:T>G-41:T>G	2A	57.4
4559480|F|0-56:G>C-56:G>C	2A	57.4
4347848|F|0-48:T>A-48:T>A	2B	0
3615705|F|0-55:C>T-55:C>T	2B	0
4348337|F|0-61:C>T-61:C>T	2B	1.1
3617148|F|0-30:G>A-30:G>A	2B	1.1
4350421|F|0-13:T>C-13:T>C	2B	2.4
4339726|F|0-8:C>T-8:C>T	2B	3.4
3616641|F|0-15:T>G-15:T>G	2B	3.9
8538689|F|0-20:A>G-20:A>G	2B	6.3
8512042|F|0-25:T>C-25:T>C	2B	10.9
8538153|F|0-13:C>G-13:C>G	2B	11.7
3040875|F|0-16:T>C-16:T>C	2B	11.7
4344073|F|0-22:C>G-22:C>G	2B	13.4
4346115|F|0-8:G>A-8:G>A	2B	13.4
4351699|F|0-8:T>G-8:T>G	2B	14.2
4339218|F|0-30:G>C-30:G>C	2B	15.6
4570925|F|0-9:G>C-9:G>C	2B	16.6
14475943|F|0-9:G>A-9:G>A	2B	18.5
4206876|F|0-32:C>G-32:C>G	2B	18.5
8512939|F|0-11:C>G-11:C>G	2B	20.1
3046566|F|0-53:A>G-53:A>G	2B	20.1
19758994|F|0-39:A>G-39:A>G	2B	23.6
4207172|F|0-28:G>C-28:G>C	2B	24.3
4369268|F|0-54:C>G-54:C>G	2B	24.7
4559885|F|0-17:G>A-17:G>A	2B	24.9
8535302|F|0-38:A>G-38:A>G	2B	28.1
4362307|F|0-10:C>T-10:C>T	2B	31
4206961|F|0-50:C>G-50:C>G	2B	32.4
8539613|F|0-7:A>G-7:A>G	2B	34
4556267|F|0-40:C>T-40:C>T	2B	34.9
8511159|F|0-11:C>T-11:C>T	2B	35.4
4214282|F|0-11:C>T-11:C>T	2B	35.6
8510655|F|0-66:G>T-66:G>T	2B	35.9
4212218|F|0-38:T>G-38:T>G	2B	36.4
4201051|F|0-15:A>G-15:A>G	2B	37.7
16357430|F|0-6:T>C-6:T>C	2B	39.6
16357430|F|0-19:T>G-19:T>G	2B	40.1
3621034|F|0-23:A>G-23:A>G	2B	40.9
4206075|F|0-60:C>G-60:C>G	2B	43.1
3043326|F|0-62:A>G-62:A>G	2B	44.9
4208676|F|0-21:G>C-21:G>C	2B	46.6
4209811|F|0-31:C>T-31:C>T	2B	47.8
3048113|F|0-32:T>G-32:T>G	2B	48.1

4207127|F|0-36:G>A-36:G>A	2B	48.4
8513007|F|0-13:A>G-13:A>G	2B	49.2
11913045|F|0-31:A>G-31:A>G	2B	49.2
8513008|F|0-34:G>A-34:G>A	2B	49.3
19759458|F|0-24:T>A-24:T>A	2B	49.3
8509816|F|0-35:A>G-35:A>G	2B	50.6
4221456|F|0-6:A>G-6:A>G	2B	50.8
4346932|F|0-24:T>G-24:T>G	2B	51.9
3040739|F|0-36:A>G-36:A>G	2B	52.9
10523135|F|0-36:G>A-36:G>A	2B	52.9
4208573|F|0-11:C>T-11:C>T	2B	53.8
3041025|F|0-45:C>G-45:C>G	2B	55.6
4372487|F|0-26:T>G-26:T>G	2B	57.6
10517361|F|0-33:T>C-33:T>C	2B	58.3
3048234|F|0-31:T>C-31:T>C	2B	58.5
3041167|F|0-65:G>T-65:G>T	2B	59.7
3046194|F|0-31:A>G-31:A>G	2B	59.7
3042042|F|0-5:T>A-5:T>A	2B	60.6
11911490|F|0-41:G>T-41:G>T	2B	60.6
11911705|F|0-32:A>G-32:A>G	2B	61
4568188|F|0-23:G>A-23:G>A	2B	64.4
10520941|F|0-30:T>C-30:T>C	2B	66.1
3040777|F|0-12:G>A-12:G>A	2B	66.2
3042051|F|0-66:G>T-66:G>T	2B	66.2
11912465|F|0-29:A>T-29:A>T	2B	67.4
3048019|F|0-8:C>T-8:C>T	2B	67.4
8534980|F|0-7:G>C-7:G>C	2B	70.3
8511413|F|0-34:A>G-34:A>G	2B	70.3
4553468|F|0-34:T>G-34:T>G	2B	71.6
4567956|F|0-17:A>G-17:A>G	2B	71.6
3042218|F|0-11:A>G-11:A>G	2B	72.4
4353437|F|0-13:G>A-13:G>A	2B	72.4
4573304|F|0-20:A>G-20:A>G	2B	73.1
3043255|F|0-41:G>A-41:G>A	2B	73.5
8511872|F|0-42:C>G-42:C>G	2B	74.9
4210752|F|0-5:C>G-5:C>G	2B	74.9
3043997|F|0-36:C>G-36:C>G	2B	76.4
3047911|F|0-22:T>C-22:T>C	2B	76.9
3045342|F|0-19:G>A-19:G>A	2B	77.8
11911498|F|0-30:A>G-30:A>G	2B	78.2
4561430|F|0-32:C>G-32:C>G	2B	79.2
4210507|F|0-17:G>A-17:G>A	2B	79.2
10519708|F|0-19:C>T-19:C>T	2B	80.6
3042584|F|0-53:A>G-53:A>G	2B	81.9
4368097|F|0-60:T>C-60:T>C	2B	82.6
3044508|F|0-15:T>C-15:T>C	2B	84.7
3617015|F|0-56:T>C-56:T>C	2B	86
8510350|F|0-18:G>C-18:G>C	2B	86.2

4564441|F|0-40:G>A-40:G>A	2B	86.7
4210797|F|0-18:T>G-18:T>G	2B	87.9
3040773|F|0-38:C>T-38:C>T	2B	90.1
3048158|F|0-25:G>A-25:G>A	2B	91.3
3044977|F|0-35:A>C-35:A>C	2B	94.4
4211419|F|0-41:T>C-41:T>C	2B	95.9
3046403|F|0-25:A>G-25:A>G	2B	97.3
3040771|F|0-59:T>C-59:T>C	2B	97.3
3044946|F|0-19:T>A-19:T>A	2B	99.9
3042556|F|0-37:A>G-37:A>G	2B	100.7
3046175|F|0-29:A>G-29:A>G	2B	100.9
3617608|F|0-12:C>G-12:C>G	2B	100.9
3605700|F|0-7:G>A-7:G>A	2B	102.9
3605484|F|0-35:A>C-35:A>C	2B	105.6
3046626|F|0-49:A>C-49:A>C	2B	107.1
8510541|F|0-15:T>C-15:T>C	2B	108.7
4557511|F|0-6:A>G-6:A>G	2B	115.1
4552964|F|0-34:T>C-34:T>C	2B	115.6
4568497|F|0-17:C>T-17:C>T	2B	115.7
4362126|F|0-24:A>G-24:A>G	2B	120.7
3047224|F|0-46:G>T-46:G>T	2B	122.5
3046048|F|0-33:G>T-33:G>T	2B	125.2
3042109|F|0-23:T>C-23:T>C	2B	135.4
4214570|F|0-65:C>T-65:C>T	2B	135.9
4349371|F|0-17:T>A-17:T>A	2B	136
8537224|F|0-10:C>G-10:C>G	2B	136
3615895|F|0-39:A>T-39:A>T	2B	136.8
4342979|F|0-18:C>T-18:C>T	2B	138.7
3043472|F|0-42:A>G-42:A>G	2B	140.4
3043752|F|0-16:C>A-16:C>A	2B	142.3
3614695|F|0-40:T>C-40:T>C	2B	145.2
16353188|F|0-39:G>C-39:G>C	2B	149.5
3043964|F|0-31:G>C-31:G>C	2B	151.9
3603506|F|0-15:G>A-15:G>A	2B	152.9
4220071|F|0-12:C>G-12:C>G	2B	153
8511843|F|0-14:G>C-14:G>C	3A	0
4213879|F|0-37:G>A-37:G>A	3A	0
10517634|F|0-19:C>T-19:C>T	3A	2.2
8532039|F|0-9:A>C-9:A>C	3A	7.6
8510462|F|0-9:A>G-9:A>G	3A	8.9
4217888|F|0-31:T>A-31:T>A	3A	14.7
4553034|F|0-56:C>T-56:C>T	3A	15.7
4212853|F|0-55:A>G-55:A>G	3A	32.6
3043783|F|0-43:A>T-43:A>T	3A	34.5
8531560|F|0-27:A>G-27:A>G	3A	42.4
4349381|F|0-9:A>G-9:A>G	3A	45.7
3046803|F|0-67:A>G-67:A>G	3A	46.5
3044881|F|0-26:G>C-26:G>C	3A	48.4

4547360|F|0-32:T>C-32:T>C	3A	52.9
3048056|F|0-13:A>C-13:A>C	3A	55.8
4209464|F|0-20:G>C-20:G>C	3A	58
3042058|F|0-32:C>G-32:C>G	3A	59
4367715|F|0-41:G>C-41:G>C	3A	61.5
4354142|F|0-9:C>T-9:C>T	3A	64.2
3615201|F|0-25:G>A-25:G>A	3A	71.3
3047299|F|0-7:A>T-7:A>T	3A	72.3
8531529|F|0-12:A>G-12:A>G	3A	73.7
8512672|F|0-8:C>G-8:C>G	3A	74.8
4546755|F|0-10:T>C-10:T>C	3A	77.2
4339717|F|0-5:C>T-5:C>T	3A	79.5
3625150|F|0-30:T>C-30:T>C	3A	81.2
3618111|F|0-6:T>C-6:T>C	3A	83
3612874|F|0-39:C>A-39:C>A	3A	86.7
3612874|F|0-14:A>G-14:A>G	3A	87.6
3041804|F|0-51:C>T-51:C>T	3A	90.1
4211984|F|0-56:G>C-56:G>C	3A	101.3
11911025|F|0-30:C>G-30:C>G	3A	107.7
4219547|F|0-7:C>T-7:C>T	3A	109.6
4370535|F|0-14:T>C-14:T>C	3A	109.6
#N/A	3B	0
#N/A	3B	35
3612466|F|0-31:A>G-31:A>G	3B	70
14479870|F|0-26:A>T-26:A>T	3B	70
3040737|F|0-45:T>G-45:T>G	3B	73.7
3603806|F|0-24:G>A-24:G>A	3B	75.8
4548433|F|0-9:A>G-9:A>G	3B	76.6
14479678|F|0-40:G>C-40:G>C	3B	78
8536359|F|0-13:T>C-13:T>C	3B	78
10522275|F|0-14:A>G-14:A>G	3B	78.2
4565144|F|0-28:T>G-28:T>G	3B	79
8539430|F|0-44:T>G-44:T>G	3B	84.4
3623465|F|0-28:A>C-28:A>C	3B	85.4
3623547|F|0-37:C>G-37:C>G	3B	85.4
10525390|F|0-10:A>G-10:A>G	3B	88
8539706|F|0-34:C>G-34:C>G	3B	88.1
10525156|F|0-33:T>C-33:T>C	3B	89.9
3623829|F|0-26:T>C-26:T>C	3B	91.7
3045739|F|0-26:C>G-26:C>G	3B	92.9
4554401|F|0-12:C>T-12:C>T	3B	92.9
14474486|F|0-20:G>C-20:G>C	3B	95.1
3613350|F|0-32:T>C-32:T>C	3B	95.3
8510168|F|0-8:A>G-8:A>G	3B	105.6
4346573|F|0-7:T>C-7:T>C	3B	107.3
3046376|F|0-5:T>C-5:T>C	3B	108.1
3046830|F|0-16:C>G-16:C>G	3B	109.9
4355510|F|0-14:G>A-14:G>A	3B	112

10507360|F|0-64:G>A-64:G>A	3B	113.4
3614684|F|0-53:G>T-53:G>T	3B	114.8
4344494|F|0-12:T>C-12:T>C	3B	114.8
3046599|F|0-25:C>T-25:C>T	3B	116.1
3040755|F|0-59:C>T-59:C>T	3B	116.2
3043854|F|0-41:A>G-41:A>G	3B	117.7
3613664|F|0-16:A>C-16:A>C	3B	120.2
4353853|F|0-14:A>G-14:A>G	3B	121.6
4200924|F|0-20:A>G-20:A>G	3B	122.9
3047112|F|0-43:C>G-43:C>G	3B	122.9
4372069|F|0-6:C>T-6:C>T	3B	123.6
3621237|F|0-13:C>G-13:C>G	3B	124.7
8510245|F|0-12:C>T-12:C>T	3B	124.7
3046248|F|0-11:C>G-11:C>G	3B	125.3
3608532|F|0-14:T>G-14:T>G	3B	129.1
4556333|F|0-13:G>A-13:G>A	3B	135.6
3624438|F|0-32:A>C-32:A>C	3B	136.8
4340546|F|0-5:T>C-5:T>C	3B	137.1
4370235|F|0-35:A>G-35:A>G	3B	137.5
8512741|F|0-6:G>A-6:G>A	3B	138.4
3613038|F|0-26:T>C-26:T>C	3B	138.4
3046789|F|0-36:A>G-36:A>G	3B	139.4
4349831|F|0-26:C>T-26:C>T	3B	141.4
3043632|F|0-23:A>C-23:A>C	3B	144.4
4206062|F|0-43:T>C-43:T>C	3B	154.2
3047385|F|0-59:T>G-59:T>G	3B	154.5
4548822|F|0-7:C>T-7:C>T	3B	155.2
3042220|F|0-29:C>T-29:C>T	3B	155.3
4566550|F|0-39:T>G-39:T>G	3B	157.3
8538315|F|0-5:G>T-5:G>T	3B	160.4
4203829|F|0-14:G>C-14:G>C	3B	162.1
3618189|F|0-15:G>A-15:G>A	3B	162.1
3045246|F|0-6:T>C-6:T>C	3R	0
15997458|F|0-12:T>C-12:T>C	3R	0
3045246|F|0-17:C>T-17:C>T	3R	1.6
3045246|F|0-28:A>T-28:A>T	3R	3.6
4213353|F|0-14:G>C-14:G>C	3R	8.6
4344210|F|0-7:T>C-7:T>C	3R	11.2
4566181|F|0-14:G>A-14:G>A	3R	14.3
3047061|F|0-13:A>G-13:A>G	3R	17.9
3047355|F|0-12:A>T-12:A>T	3R	20.9
4347109|F|0-24:G>T-24:G>T	3R	21.7
8511310|F|0-7:C>G-7:C>G	3R	25.3
11912946|F|0-36:A>T-36:A>T	3R	26.9
4364898|F|0-14:G>A-14:G>A	3R	27.5
3041974|F|0-58:A>G-58:A>G	3R	30.8
3043993|F|0-18:T>A-18:T>A	3R	33.5
3045879|F|0-13:A>G-13:A>G	3R	36.9

3619095|F|0-36:C>A-36:C>A	3R	38.1
8539707|F|0-12:A>G-12:A>G	3R	40.3
4342398|F|0-16:G>C-16:G>C	3R	43.4
3042536|F|0-38:G>A-38:G>A	3R	46.5
4345422|F|0-18:T>G-18:T>G	3R	49.1
4364530|F|0-11:G>A-11:G>A	3R	52.5
8539235|F|0-16:G>C-16:G>C	3R	56.2
8510200|F|0-13:G>C-13:G>C	3R	57.6
3622301|F|0-32:T>C-32:T>C	3R	60.4
4206106|F|0-65:A>C-65:A>C	3R	63.1
4203972|F|0-42:T>G-42:T>G	3R	64.3
4339956|F|0-17:C>G-17:C>G	3R	67.3
3604338|F|0-21:A>G-21:A>G	3R	70.2
8512645|F|0-49:G>C-49:G>C	3R	72
3047298|F|0-29:C>A-29:C>A	3R	74
4351063|F|0-11:C>G-11:C>G	3R	75.5
4563779|F|0-22:T>C-22:T>C	3R	77.3
3620862|F|0-37:T>C-37:T>C	3R	79.1
8539394|F|0-31:C>T-31:C>T	3R	81.2
4217529|F|0-34:C>G-34:C>G	3R	83.5
4212902|F|0-24:T>A-24:T>A	3R	86.2
3046550|F|0-17:C>G-17:C>G	3R	87.3
3620134|F|0-35:G>A-35:G>A	3R	98.9
10522294|F|0-25:T>C-25:T>C	3R	101.5
8512498|F|0-7:G>T-7:G>T	3R	103.6
4567505|F|0-20:C>T-20:C>T	3R	109.1
3611904|F|0-24:T>C-24:T>C	3R	109.4
3609517|F|0-12:C>T-12:C>T	3R	114.7
4350385|F|0-22:C>A-22:C>A	3R	119.6
4553801|F|0-8:T>C-8:T>C	3R	121
4369932|F|0-13:T>C-13:T>C	3R	127.2
4205637|F|0-44:G>A-44:G>A	3R	130.1
4212188|F|0-19:A>G-19:A>G	3R	135
4340256|F|0-10:C>A-10:C>A	3R	138.8
3048201|F|0-14:A>C-14:A>C	3R	140.9
4221330|F|0-19:T>G-19:T>G	3R	144.2
4202609|F|0-23:G>C-23:G>C	3R	146.5
4566784|F|0-13:A>G-13:A>G	3R	148.8
15998554|F|0-5:A>T-5:A>T	3R	151.2
4352526|F|0-9:C>A-9:C>A	3R	153
4368567|F|0-67:C>T-67:C>T	3R	153.9
4368567|F|0-63:T>A-63:T>A	3R	156.2
4367301|F|0-16:C>G-16:C>G	3R	156.2
3046429|F|0-20:T>G-20:T>G	4A	0
8531377|F|0-33:A>G-33:A>G	4A	0.1
4353110|F|0-22:A>G-22:A>G	4A	1.3
3040547|F|0-35:T>C-35:T>C	4A	3.2
4367675|F|0-40:A>T-40:A>T	4A	4.2

3045803|F|0-38:C>G-38:C>G	4A	5.9
10523626|F|0-38:C>T-38:C>T	4A	8.8
14475485|F|0-8:A>G-8:A>G	4A	9.1
8531741|F|0-22:G>A-22:G>A	4A	11
8531145|F|0-12:G>A-12:G>A	4A	11.7
4346903|F|0-10:G>A-10:G>A	4A	14
3043139|F|0-41:C>A-41:C>A	4A	17.4
4355703|F|0-28:C>G-28:C>G	4A	18.5
19759466|F|0-18:A>T-18:A>T	4A	19.7
19759466|F|0-28:G>C-28:G>C	4A	20.7
4369437|F|0-21:A>G-21:A>G	4A	24.2
4369839|F|0-27:A>C-27:A>C	4A	24.2
4369352|F|0-21:A>G-21:A>G	4A	28.3
8512312|F|0-22:C>T-22:C>T	4A	32.2
3041767|F|0-37:C>T-37:C>T	4A	33.3
4367834|F|0-38:G>C-38:G>C	4A	35.9
4548995|F|0-52:A>G-52:A>G	4A	38.3
4356532|F|0-26:G>C-26:G>C	4A	40.3
8510272|F|0-23:C>T-23:C>T	4A	40.8
4370148|F|0-23:A>G-23:A>G	4A	42.4
4342671|F|0-45:T>C-45:T>C	4A	43.7
3041339|F|0-29:T>C-29:T>C	4A	45.7
3041011|F|0-49:G>T-49:G>T	4A	47.4
4370576|F|0-13:T>G-13:T>G	4A	48.7
4219108|F|0-12:G>T-12:G>T	4A	50
4212915|F|0-65:G>C-65:G>C	4A	51.4
4370642|F|0-32:G>C-32:G>C	4A	53.7
4351282|F|0-44:C>G-44:C>G	4A	56.8
4345593|F|0-21:G>C-21:G>C	4A	58.9
10525079|F|0-5:C>A-5:C>A	4A	70
11912332|F|0-20:C>G-20:C>G	4A	72.9
4574060|F|0-5:T>C-5:T>C	4A	73.7
16354127|F|0-18:C>T-18:C>T	4A	75.1
4554644|F|0-20:C>T-20:C>T	4A	77.1
4359204|F|0-43:C>G-43:C>G	4A	79.2
10519071|F|0-7:G>A-7:G>A	4A	80.4
4357772|F|0-16:A>G-16:A>G	4A	81
4373475|F|0-22:G>C-22:G>C	4A	82.5
8512449|F|0-27:A>G-27:A>G	4A	85.5
4365044|F|0-8:C>T-8:C>T	4A	94.5
8512212|F|0-13:G>C-13:G>C	4A	94.8
3041112|F|0-26:G>A-26:G>A	4B	0
8511249|F|0-10:C>G-10:C>G	4B	0
3620552|F|0-31:G>C-31:G>C	4B	3.2
4348275|F|0-6:C>T-6:C>T	4B	5.3
10521898|F|0-31:G>A-31:G>A	4B	14.5
4206295|F|0-27:C>G-27:C>G	4B	18.7
3613355|F|0-23:A>G-23:A>G	4B	18.7

10525143|F|0-37:T>C-37:T>C	4R	0
8512478|F|0-25:G>C-25:G>C	4R	0
8538981|F|0-11:A>G-11:A>G	4R	2.7
4346013|F|0-8:T>C-8:T>C	4R	6.4
4561347|F|0-47:C>A-47:C>A	4R	8.8
4361147|F|0-14:G>A-14:G>A	4R	12.2
4217801|F|0-22:C>G-22:C>G	4R	15.7
3040707|F|0-59:C>G-59:C>G	4R	18.9
3611538|F|0-20:T>G-20:T>G	4R	20.9
3617141|F|0-26:A>T-26:A>T	4R	22.9
3619045|F|0-27:G>T-27:G>T	4R	24.9
3615065|F|0-44:G>C-44:G>C	4R	27.1
3047932|F|0-17:A>C-17:A>C	4R	29.8
8512172|F|0-20:C>G-20:C>G	4R	33.1
4359649|F|0-15:A>G-15:A>G	4R	37.2
3042608|F|0-65:C>T-65:C>T	4R	42.1
3605534|F|0-8:C>T-8:C>T	4R	47.1
4355139|F|0-5:T>C-5:T>C	4R	49.7
4347589|F|0-14:G>A-14:G>A	4R	52.1
4372942|F|0-9:C>T-9:C>T	4R	54.8
4371106|F|0-46:G>A-46:G>A	4R	56
3618899|F|0-8:G>C-8:G>C	4R	58.6
3047933|F|0-16:C>T-16:C>T	4R	61.5
8510991|F|0-14:C>T-14:C>T	4R	63.3
3043545|F|0-60:T>G-60:T>G	4R	64.4
3048121|F|0-42:T>C-42:T>C	4R	65.9
4342961|F|0-7:A>G-7:A>G	4R	68.2
4575472|F|0-54:A>C-54:A>C	4R	70.2
4359903|F|0-51:G>C-51:G>C	4R	74.7
3040828|F|0-33:C>T-33:C>T	4R	77.7
3617716|F|0-20:A>G-20:A>G	4R	78.2
10519396|F|0-10:A>G-10:A>G	5A	0
3618419|F|0-12:C>T-12:C>T	5A	6.6
4564410|F|0-5:T>C-5:T>C	5A	10.2
3048231|F|0-59:A>G-59:A>G	5A	13
8510566|F|0-24:T>C-24:T>C	5A	14.1
4369809|F|0-25:C>T-25:C>T	5A	14.7
3043838|F|0-24:T>C-24:T>C	5A	17.2
8510713|F|0-67:G>A-67:G>A	5A	25.3
3045041|F|0-6:G>C-6:G>C	5A	28.1
4352816|F|0-7:A>G-7:A>G	5A	35.1
8509821|F|0-5:T>C-5:T>C	5A	36.7
4361203|F|0-42:G>T-42:G>T	5A	37.4
3616438|F|0-45:C>T-45:C>T	5A	38.7
3045186|F|0-23:C>G-23:C>G	5A	41.8
11910690|F|0-10:A>G-10:A>G	5A	50.7
4368543|F|0-12:T>C-12:T>C	5A	53.8
3047420|F|0-46:T>C-46:T>C	5A	55.2

3041628|F|0-34:A>G-34:A>G	5A	56.9
3043887|F|0-43:T>C-43:T>C	5A	60.3
3043111|F|0-18:A>G-18:A>G	5A	66.8
14476192|F|0-16:G>A-16:G>A	5A	72
4369428|F|0-18:T>C-18:T>C	5A	76.1
10510387|F|0-11:G>A-11:G>A	5A	86.3
8510980|F|0-43:C>T-43:C>T	5A	90.5
4211970|F|0-17:G>C-17:G>C	5A	100.4
19758850|F|0-25:T>C-25:T>C	5A	121.3
4345993|F|0-50:C>T-50:C>T	5A	129.9
8511982|F|0-33:T>C-33:T>C	5A	134.2
4208849|F|0-14:T>G-14:T>G	5A	143.3
4340705|F|0-24:A>T-24:A>T	5A	146.1
3047343|F|0-35:A>G-35:A>G	5A	147.4
3044232|F|0-20:G>T-20:G>T	5A	150.6
3612827|F|0-13:T>C-13:T>C	5A	158.5
3622389|F|0-26:T>G-26:T>G	5A	160.3
3043615|F|0-6:C>G-6:C>G	5A	161.4
4209303|F|0-13:C>G-13:C>G	5A	168.9
4209786|F|0-20:T>A-20:T>A	5A	171
8511754|F|0-8:T>C-8:T>C	5A	173.5
8511754|F|0-18:A>G-18:A>G	5A	174.7
4341775|F|0-14:G>A-14:G>A	5A	176.5
3046539|F|0-63:T>C-63:T>C	5B	0
16356784|F|0-38:C>T-38:C>T	5B	0
3604139|F|0-9:C>T-9:C>T	5B	2.1
4545148|F|0-17:G>A-17:G>A	5B	5.6
10514019|F|0-38:A>G-38:A>G	5B	15.1
4358998|F|0-6:A>G-6:A>G	5B	19.3
3041856|F|0-19:T>G-19:T>G	5B	20.7
3604550|F|0-9:C>T-9:C>T	5B	23.1
4361241|F|0-31:C>T-31:C>T	5B	29.6
3040857|F|0-20:A>T-20:A>T	5B	30.7
3606982|F|0-35:C>T-35:C>T	5B	31.1
4348097|F|0-22:G>T-22:G>T	5B	33.1
4201091|F|0-11:A>C-11:A>C	5B	36.8
3046632|F|0-31:T>A-31:T>A	5B	39.6
3046870|F|0-37:A>C-37:A>C	5B	40.8
4205783|F|0-8:C>T-8:C>T	5B	43.6
3041175|F|0-41:T>G-41:T>G	5B	46.9
8511755|F|0-5:T>G-5:T>G	5B	49.3
3043601|F|0-36:A>G-36:A>G	5B	52.8
4212028|F|0-12:A>T-12:A>T	5B	54.6
8511160|F|0-8:C>T-8:C>T	5B	59.5
3616991|F|0-22:C>T-22:C>T	5B	64.1
3040826|F|0-35:T>C-35:T>C	5B	66.7
3044020|F|0-23:A>G-23:A>G	5B	67.8
4215435|F|0-6:C>G-6:C>G	5B	70.7

3048151|F|0-50:C>T-50:C>T	5B	72.7
3041052|F|0-59:C>T-59:C>T	5B	86.8
3617440|F|0-25:A>C-25:A>C	5B	91.7
4370137|F|0-25:G>A-25:G>A	5B	94
3040898|F|0-19:A>T-19:A>T	5B	96.5
4355792|F|0-27:C>T-27:C>T	5B	96.5
3045969|F|0-46:C>T-46:C>T	5B	99.1
3617595|F|0-6:A>C-6:A>C	5B	100
3616595|F|0-13:A>G-13:A>G	5B	103.4
4368831|F|0-24:C>T-24:C>T	5B	106.9
3045796|F|0-16:T>C-16:T>C	5B	111.6
4369135|F|0-22:G>A-22:G>A	5B	114.7
8511371|F|0-11:C>A-11:C>A	5B	117.6
4352292|F|0-31:C>G-31:C>G	5B	118.8
3041304|F|0-31:G>A-31:G>A	5B	121.2
4369938|F|0-35:G>C-35:G>C	5B	121.2
4365926|F|0-22:C>T-22:C>T	5B	124.1
10522138|F|0-6:A>G-6:A>G	5B	125.1
4207594|F|0-31:T>G-31:T>G	5B	127.6
4368328|F|0-34:G>A-34:G>A	5B	133.6
4368320|F|0-6:C>T-6:C>T	5B	137.1
8511122|F|0-22:C>G-22:C>G	5B	146.8
4213924|F|0-7:C>T-7:C>T	5B	148.7
16353769|F|0-13:A>G-13:A>G	5B	151
4212242|F|0-45:T>C-45:T>C	5B	153.4
4209975|F|0-45:G>T-45:G>T	5B	155.5
3041371|F|0-13:C>T-13:C>T	5B	156
3046072|F|0-39:C>G-39:C>G	5B	159.8
4356684|F|0-11:C>G-11:C>G	5B	161.9
8538138|F|0-17:C>T-17:C>T	5B	165.7
4204408|F|0-34:T>C-34:T>C	5B	173.3
3045122|F|0-8:C>T-8:C>T	5B	176.5
4216635|F|0-10:T>C-10:T>C	5B	179.5
15997669|F|0-25:C>G-25:C>G	5B	183
4355220|F|0-14:T>C-14:T>C	5B	185.1
4547103|F|0-17:A>G-17:A>G	5B	188.8
4570434|F|0-6:G>T-6:G>T	5B	192
10508430|F|0-23:T>A-23:T>A	5B	193.4
3621724|F|0-35:T>G-35:T>G	5B	199.3
4208972|F|0-17:T>G-17:T>G	5B	200.2
4211640|F|0-10:G>A-10:G>A	5B	201.8
4361014|F|0-42:G>C-42:G>C	5B	205.2
4212676|F|0-42:G>C-42:G>C	5B	209.9
11910489|F|0-30:C>T-30:C>T	5B	212.3
4349976|F|0-16:G>T-16:G>T	5B	214.9
4554662|F|0-10:T>C-10:T>C	5B	216.2
4353104|F|0-12:G>A-12:G>A	5B	218
4573292|F|0-33:C>T-33:C>T	5B	218

8537991|F|0-19:T>C-19:T>C	5R	23.3
4217803|F|0-32:A>G-32:A>G	5R	26.7
16312805|F|0-9:A>C-9:A>C	5R	27.8
4368305|F|0-34:G>C-34:G>C	5R	31.1
4368984|F|0-41:G>A-41:G>A	5R	38.9
10511847|F|0-30:G>C-30:G>C	5R	41.4
4349077|F|0-16:A>G-16:A>G	5R	43.9
10509424|F|0-13:A>T-13:A>T	5R	70.7
4212683|F|0-12:G>C-12:G>C	5R	73.8
4354271|F|0-37:G>C-37:G>C	5R	74.9
4339290|F|0-10:G>C-10:G>C	5R	77.2
4218413|F|0-29:G>T-29:G>T	5R	80.3
8537234|F|0-28:A>C-28:A>C	5R	82.2
8511829|F|0-24:G>C-24:G>C	5R	86.3
4203295|F|0-11:T>A-11:T>A	5R	89.6
4370061|F|0-47:C>G-47:C>G	5R	92.3
3047741|F|0-43:C>A-43:C>A	5R	94.2
4210475|F|0-54:T>C-54:T>C	5R	97
8535839|F|0-9:C>G-9:C>G	5R	102.5
3044240|F|0-45:C>G-45:C>G	5R	109
4551383|F|0-32:G>C-32:G>C	5R	114.4
4358372|F|0-13:T>G-13:T>G	5R	118.2
4200926|F|0-6:T>C-6:T>C	5R	123.7
4550653|F|0-16:G>C-16:G>C	5R	154.7
3622112|F|0-32:A>C-32:A>C	5R	160.6
3616689|F|0-13:G>C-13:G>C	5R	165.8
3043065|F|0-17:C>T-17:C>T	5R	171.7
4372334|F|0-23:C>T-23:C>T	5R	177.2
4548418|F|0-7:G>A-7:G>A	5R	183.2
3604134|F|0-27:G>A-27:G>A	5R	186.3
4572801|F|0-26:G>A-26:G>A	5R	189.7
3615271|F|0-15:G>C-15:G>C	5R	191.3
8511622|F|0-5:C>A-5:C>A	5R	196
8533380|F|0-13:C>G-13:C>G	5R	198.4
10511507|F|0-5:T>A-5:T>A	5R	203.4
4215609|F|0-37:G>A-37:G>A	5R	208
4215785|F|0-9:T>G-9:T>G	5R	210.3
8510762|F|0-17:C>T-17:C>T	5R	211.9
3040767|F|0-6:C>T-6:C>T	5R	213.3
3041225|F|0-17:T>A-17:T>A	5R	214.7
4358777|F|0-13:T>G-13:T>G	5R	219.7
15998544|F|0-21:G>C-21:G>C	5R	222.3
10507075|F|0-66:G>C-66:G>C	5R	224.7
3045634|F|0-14:C>G-14:C>G	5R	228
3622528|F|0-59:T>C-59:T>C	5R	232.3
8511119|F|0-12:G>T-12:G>T	5R	233.4
3047904|F|0-50:C>G-50:C>G	5R	236.1
3044647|F|0-9:A>G-9:A>G	5R	237

3608227|F|0-48:G>A-48:G>A	5R	239
4212656|F|0-33:G>A-33:G>A	5R	243.1
3609381|F|0-24:A>G-24:A>G	5R	248.6
4350371|F|0-34:G>C-34:G>C	5R	253.5
3609249|F|0-8:C>T-8:C>T	5R	258.1
4344453|F|0-14:A>T-14:A>T	5R	260.4
3613416|F|0-6:T>A-6:T>A	5R	263.8
4221573|F|0-11:C>A-11:C>A	5R	266.6
4201323|F|0-11:T>G-11:T>G	5R	268.9
3047898|F|0-32:A>C-32:A>C	5R	273.5
4368983|F|0-13:C>G-13:C>G	5R	277.5
4574651|F|0-7:A>G-7:A>G	5R	281.2
3622843|F|0-45:G>C-45:G>C	5R	288
3617575|F|0-19:T>A-19:T>A	5R	294.2
3040766|F|0-12:A>C-12:A>C	5R	297.1
8511804|F|0-6:A>G-6:A>G	5R	298.4
3044663|F|0-29:C>G-29:C>G	5R	301
3042635|F|0-56:G>T-56:G>T	5R	307.3
8538038|F|0-15:C>T-15:C>T	5R	310.7
4211525|F|0-8:A>G-8:A>G	5R	313
16358671|F|0-14:A>C-14:A>C	5R	318
4204938|F|0-37:C>T-37:C>T	5R	325.7
4209185|F|0-53:C>T-53:C>T	5R	330.7
10524133|F|0-33:C>T-33:C>T	5R	333.9
14479933|F|0-8:C>A-8:C>A	5R	335.8
10521057|F|0-10:A>C-10:A>C	5R	338.5
4203815|F|0-10:A>G-10:A>G	5R	344.6
4349596|F|0-19:A>G-19:A>G	5R	347.5
3616658|F|0-7:T>C-7:T>C	5R	352.3
3606139|F|0-6:T>C-6:T>C	5R	356.4
4343052|F|0-32:T>C-32:T>C	5R	361.9
10508847|F|0-59:T>C-59:T>C	5R	367.8
8536312|F|0-14:G>C-14:G>C	5R	371.3
3046635|F|0-24:C>G-24:C>G	5R	374.3
4367448|F|0-22:G>A-22:G>A	5R	378.1
4207009|F|0-34:A>G-34:A>G	5R	383.8
8510389|F|0-8:C>T-8:C>T	5R	387.7
3047607|F|0-13:A>G-13:A>G	5R	393
8512716|F|0-11:G>C-11:G>C	5R	398.6
8512219|F|0-18:A>C-18:A>C	5R	406.2
3045359|F|0-19:T>C-19:T>C	5R	408.6
4217463|F|0-37:G>A-37:G>A	5R	412.1
3614060|F|0-19:A>C-19:A>C	5R	418.5
3046717|F|0-15:C>T-15:C>T	5R	422.5
8535875|F|0-11:G>T-11:G>T	5R	425.6
8537412|F|0-7:T>G-7:T>G	5R	428.4
4352671|F|0-16:A>C-16:A>C	5R	432.1
4212674|F|0-32:G>T-32:G>T	5R	435.9

10514813|F|0-11:C>T-11:C>T	5R	438.3
4215269|F|0-13:C>G-13:C>G	5R	444
4369388|F|0-16:C>G-16:C>G	5R	448.9
4342343|F|0-17:A>G-17:A>G	5R	452.6
4364388|F|0-22:C>T-22:C>T	5R	456.2
4573634|F|0-16:C>T-16:C>T	5R	461.8
16356839|F|0-50:G>A-50:G>A	5R	464.1
4370143|F|0-56:T>A-56:T>A	5R	465.8
3624076|F|0-23:G>A-23:G>A	5R	468
10522522|F|0-14:C>G-14:C>G	5R	471
3047859|F|0-32:A>T-32:A>T	5R	476
4372582|F|0-6:C>G-6:C>G	5R	479.4
4364448|F|0-9:G>C-9:G>C	5R	482.9
8537768|F|0-18:T>C-18:T>C	5R	485.7
8511234|F|0-17:T>G-17:T>G	5R	487.9
3040907|F|0-61:G>A-61:G>A	5R	494
4202361|F|0-25:A>G-25:A>G	5R	497.2
4372974|F|0-22:C>G-22:C>G	5R	499.5
3618447|F|0-64:C>G-64:C>G	5R	501.7
4565197|F|0-58:G>A-58:G>A	5R	505.9
8512116|F|0-16:G>C-16:G>C	5R	513.5
8538556|F|0-46:A>C-46:A>C	5R	515.8
4354447|F|0-68:C>G-68:C>G	5R	517.4
10523972|F|0-5:C>T-5:C>T	5R	519.1
3616194|F|0-14:C>T-14:C>T	5R	523.5
3041059|F|0-29:C>A-29:C>A	5R	526.8
3617226|F|0-11:T>C-11:T>C	5R	531
16356147|F|0-12:A>T-12:A>T	5R	532.9
8509926|F|0-53:G>C-53:G>C	5R	534.5
3047517|F|0-15:T>G-15:T>G	5R	538.5
3610593|F|0-19:G>A-19:G>A	5R	542.2
3603279|F|0-29:A>G-29:A>G	5R	546.6
3040700|F|0-39:T>C-39:T>C	5R	550
8512294|F|0-23:G>A-23:G>A	5R	551.1
3041407|F|0-31:C>T-31:C>T	5R	553.3
8510344|F|0-5:T>C-5:T>C	5R	557.3
4214907|F|0-31:A>C-31:A>C	5R	559.7
4342949|F|0-42:G>A-42:G>A	5R	562.5
3041126|F|0-31:A>G-31:A>G	5R	565.3
3613461|F|0-15:T>C-15:T>C	5R	568.4
3048220|F|0-5:T>C-5:T>C	5R	572.1
3040626|F|0-29:G>A-29:G>A	5R	576.5
4574517|F|0-10:T>C-10:T>C	5R	578.8
10522108|F|0-7:A>G-7:A>G	5R	581
4572546|F|0-16:A>G-16:A>G	5R	584
8535039|F|0-40:G>C-40:G>C	5R	585.8
4340006|F|0-12:G>A-12:G>A	5R	590.1
8512249|F|0-60:G>A-60:G>A	5R	594.3

3046661|F|0-67:A>G-67:A>G	5R	600.2
8510938|F|0-19:T>G-19:T>G	5R	605.1
4204965|F|0-60:C>T-60:C>T	5R	607.5
4564540|F|0-30:T>C-30:T>C	5R	611.1
3041928|F|0-30:A>G-30:A>G	5R	616.3
3620241|F|0-14:G>A-14:G>A	5R	623.6
3042949|F|0-6:T>C-6:T>C	6A	0
4355804|F|0-11:T>G-11:T>G	6A	0
4219305|F|0-11:A>G-11:A>G	6A	2.8
4205867|F|0-36:G>C-36:G>C	6A	4.8
4573562|F|0-62:G>A-62:G>A	6A	7.2
3042381|F|0-16:G>C-16:G>C	6A	9.7
3616875|F|0-32:G>T-32:G>T	6A	12
4370194|F|0-6:C>T-6:C>T	6A	15.3
3046108|F|0-58:A>G-58:A>G	6A	19.2
3041585|F|0-53:A>G-53:A>G	6A	25
3045307|F|0-22:A>G-22:A>G	6A	26.1
4220722|F|0-36:C>T-36:C>T	6A	30.4
3605407|F|0-32:G>A-32:G>A	6A	39.2
8535176|F|0-22:G>A-22:G>A	6A	41.8
3619256|F|0-44:C>G-44:C>G	6A	44
3048122|F|0-15:T>C-15:T>C	6A	47.5
4563504|F|0-35:C>A-35:C>A	6A	49.5
10522459|F|0-21:T>A-21:T>A	6A	52.2
3044473|F|0-8:T>C-8:T>C	6A	55.8
4346124|F|0-16:C>T-16:C>T	6A	67.6
4369619|F|0-64:T>A-64:T>A	6A	69.2
4217312|F|0-13:T>G-13:T>G	6A	75.3
3616261|F|0-30:T>C-30:T>C	6A	76.7
8510976|F|0-15:G>A-15:G>A	6A	77.1
4348315|F|0-36:A>T-36:A>T	6A	79.5
4370991|F|0-30:C>G-30:C>G	6A	80.1
4361034|F|0-5:C>T-5:C>T	6A	80.1
8537816|F|0-7:C>G-7:C>G	6A	82.9
16353862|F|0-15:G>T-15:G>T	6A	83
4371420|F|0-46:A>G-46:A>G	6A	83.8
4559296|F|0-35:T>C-35:T>C	6A	85.5
3043600|F|0-52:T>C-52:T>C	6A	85.9
4370643|F|0-53:A>G-53:A>G	6A	87.9
4359171|F|0-22:A>T-22:A>T	6A	89.7
4372709|F|0-50:C>G-50:C>G	6A	90.3
8512239|F|0-36:A>G-36:A>G	6A	91.7
4352904|F|0-28:C>A-28:C>A	6A	93.7
4354371|F|0-17:T>C-17:T>C	6A	94.7
8512122|F|0-17:C>T-17:C>T	6A	96.4
4370012|F|0-22:G>C-22:G>C	6A	97.5
16352704|F|0-57:C>G-57:C>G	6A	98.9
8512561|F|0-19:C>T-19:C>T	6A	99.4

4339927|F|0-26:G>T-26:G>T	6A	103.1
4369895|F|0-34:G>A-34:G>A	6A	106.5
4372775|F|0-20:A>C-20:A>C	6A	107.4
4345082|F|0-45:T>G-45:T>G	6A	109.3
8510426|F|0-25:C>A-25:C>A	6A	111.2
4367903|F|0-32:A>G-32:A>G	6A	115.6
4368532|F|0-18:T>C-18:T>C	6A	118.4
3047772|F|0-37:C>G-37:C>G	6A	121.8
4347189|F|0-28:G>C-28:G>C	6A	128.4
4214406|F|0-9:A>G-9:A>G	6A	128.9
3042080|F|0-33:T>G-33:T>G	6A	129.8
10523980|F|0-56:G>A-56:G>A	6A	129.9
3048147|F|0-32:G>A-32:G>A	6A	131.8
4216919|F|0-26:A>G-26:A>G	6A	134.1
3042098|F|0-10:T>C-10:T>C	6A	134.8
3044734|F|0-29:T>C-29:T>C	6A	139.1
8536000|F|0-7:C>G-7:C>G	6A	142.2
4217955|F|0-7:C>T-7:C>T	6A	144.9
4208740|F|0-35:A>T-35:A>T	6A	147.2
4212216|F|0-38:C>G-38:C>G	6A	149.4
4204993|F|0-5:G>A-5:G>A	6A	149.4
8538321|F|0-17:A>G-17:A>G	6A	150.1
4563343|F|0-47:G>C-47:G>C	6A	152.2
19759492|F|0-62:G>C-62:G>C	6A	154.9
4201097|F|0-22:G>A-22:G>A	6A	158.2
3043321|F|0-41:C>T-41:C>T	6B	0
3617246|F|0-34:C>G-34:C>G	6B	0
10519034|F|0-27:G>C-27:G>C	6B	3.6
3042697|F|0-26:C>A-26:C>A	6B	5.8
8511559|F|0-41:T>A-41:T>A	6B	8.6
3043152|F|0-14:T>G-14:T>G	6B	9.6
3046452|F|0-66:T>C-66:T>C	6B	9.6
3043376|F|0-31:C>T-31:C>T	6B	13.4
4566629|F|0-48:G>A-48:G>A	6B	23.6
4212490|F|0-37:C>T-37:C>T	6B	24.3
3619611|F|0-12:A>G-12:A>G	6B	27.3
3048114|F|0-21:G>A-21:G>A	6B	29.3
4210584|F|0-42:G>A-42:G>A	6B	31.2
4211674|F|0-6:C>G-6:C>G	6B	32.6
3617467|F|0-9:G>A-9:G>A	6B	34
4563987|F|0-26:A>G-26:A>G	6B	37
3047568|F|0-19:A>C-19:A>C	6B	40.7
3608990|F|0-8:G>T-8:G>T	6B	41.7
10520828|F|0-11:T>G-11:T>G	6B	44.5
10519425|F|0-14:T>A-14:T>A	6B	51.5
4563899|F|0-5:C>G-5:C>G	6B	53.3
3608044|F|0-30:T>C-30:T>C	6B	54.9
4575464|F|0-10:C>A-10:C>A	6B	58.3

10524139|F|0-25:A>G-25:A>G	6B	61.9
3621401|F|0-56:T>C-56:T>C	6B	67.9
4359637|F|0-33:T>C-33:T>C	6B	70.1
10516826|F|0-34:G>A-34:G>A	6B	71.8
4556969|F|0-21:G>A-21:G>A	6B	77.2
4212127|F|0-23:G>T-23:G>T	6B	78.1
3047739|F|0-59:C>T-59:C>T	6B	84.6
8511605|F|0-6:C>T-6:C>T	6B	85.9
4566170|F|0-33:G>A-33:G>A	6B	87.9
3607758|F|0-12:G>C-12:G>C	6B	90.5
3607758|F|0-33:G>C-33:G>C	6B	92.5
4373478|F|0-29:G>C-29:G>C	6B	95.8
3622659|F|0-10:G>A-10:G>A	6B	97.7
3616427|F|0-29:G>C-29:G>C	6B	98.8
3614507|F|0-8:C>G-8:C>G	6B	99.3
3617951|F|0-9:G>C-9:G>C	6B	100.4
8536309|F|0-29:G>T-29:G>T	6B	102.4
4369340|F|0-30:G>A-30:G>A	6B	105.4
3042198|F|0-12:C>T-12:C>T	6B	108.2
8539397|F|0-5:G>A-5:G>A	6B	111.2
4549524|F|0-54:C>G-54:C>G	6B	112.3
10520852|F|0-8:A>G-8:A>G	6B	114.2
10516487|F|0-14:A>C-14:A>C	6B	115.7
4354651|F|0-8:C>T-8:C>T	6B	115.7
3044986|F|0-33:C>T-33:C>T	6R	0
3042969|F|0-58:A>G-58:A>G	6R	0
3046532|F|0-15:G>A-15:G>A	6R	1.6
8538394|F|0-16:C>T-16:C>T	6R	3.2
16358604|F|0-14:G>A-14:G>A	6R	6
3047747|F|0-29:C>G-29:C>G	6R	9.2
4347749|F|0-25:C>T-25:C>T	6R	9.8
3047697|F|0-26:C>G-26:C>G	6R	13.1
3042393|F|0-48:A>T-48:A>T	6R	13.4
3605287|F|0-50:G>A-50:G>A	6R	14.3
3605287|F|0-21:G>T-21:G>T	6R	15.4
3612904|F|0-27:C>A-27:C>A	6R	15.5
3041428|F|0-5:G>A-5:G>A	6R	17.2
3047790|F|0-8:C>G-8:C>G	6R	19.5
3047567|F|0-37:C>G-37:C>G	6R	22.7
3613438|F|0-12:A>C-12:A>C	6R	25.2
4548356|F|0-6:G>T-6:G>T	6R	26.9
3612340|F|0-43:G>A-43:G>A	6R	27.5
10523826|F|0-9:T>C-9:T>C	6R	29.9
8510548|F|0-16:C>T-16:C>T	6R	31.7
10508112|F|0-29:C>T-29:C>T	6R	34.4
3616856|F|0-30:C>A-30:C>A	6R	36.3
3040597|F|0-22:A>T-22:A>T	6R	38.7
3040597|F|0-12:G>T-12:G>T	6R	41.7

3617977|F|0-40:T>G-40:T>G	6R	45.2
4211242|F|0-42:A>C-42:A>C	6R	55.9
3046454|F|0-21:T>A-21:T>A	6R	56.4
3047563|F|0-52:C>T-52:C>T	6R	57.3
3042616|F|0-14:C>T-14:C>T	6R	58.5
3624101|F|0-18:T>A-18:T>A	6R	62.3
10522424|F|0-23:G>C-23:G>C	6R	64.2
8511028|F|0-50:T>C-50:T>C	6R	67
4200883|F|0-10:C>G-10:C>G	6R	70.3
4353089|F|0-12:T>A-12:T>A	6R	72.3
4208932|F|0-14:G>C-14:G>C	6R	73.4
4345079|F|0-25:A>G-25:A>G	6R	75.2
3623977|F|0-26:G>A-26:G>A	6R	80
4207193|F|0-14:T>A-14:T>A	6R	82.4
4345860|F|0-13:C>T-13:C>T	6R	85.4
8512750|F|0-13:G>C-13:G>C	6R	86
10522910|F|0-10:G>A-10:G>A	6R	87.2
4218934|F|0-19:T>A-19:T>A	6R	88
4212809|F|0-48:C>T-48:C>T	6R	90.1
4212809|F|0-52:G>A-52:G>A	6R	91.3
4212809|F|0-35:C>G-35:C>G	6R	93.3
10522577|F|0-7:G>A-7:G>A	6R	95.1
4570016|F|0-8:G>A-8:G>A	6R	98.1
8511931|F|0-9:T>C-9:T>C	6R	100.3
3042028|F|0-19:G>C-19:G>C	6R	102.4
10525243|F|0-48:G>C-48:G>C	6R	104.2
8510384|F|0-11:C>G-11:C>G	6R	105.1
3043449|F|0-10:T>G-10:T>G	6R	106.7
4349563|F|0-27:T>C-27:T>C	6R	109.5
8537923|F|0-23:G>T-23:G>T	6R	110.2
4566474|F|0-33:C>T-33:C>T	6R	131.6
3048071|F|0-29:T>G-29:T>G	6R	133.7
3609161|F|0-44:C>A-44:C>A	6R	135.2
11911840|F|0-26:T>G-26:T>G	6R	136
4214383|F|0-23:A>T-23:A>T	6R	137.8
4206627|F|0-32:T>C-32:T>C	6R	139.7
4545735|F|0-7:T>G-7:T>G	6R	141
3606883|F|0-13:T>C-13:T>C	6R	141.9
4351501|F|0-57:A>G-57:A>G	6R	148.6
8512338|F|0-5:G>C-5:G>C	6R	150.5
3611484|F|0-37:T>C-37:T>C	6R	151.4
8535372|F|0-33:T>C-33:T>C	6R	154.9
16355629|F|0-18:A>C-18:A>C	6R	155.6
3045882|F|0-55:G>A-55:G>A	6R	159.4
8536510|F|0-12:T>C-12:T>C	6R	161.7
8510419|F|0-14:G>A-14:G>A	6R	165.7
4556715|F|0-24:T>A-24:T>A	6R	169.2
4341169|F|0-7:T>G-7:T>G	6R	170.4

10523766|F|0-66:A>G-66:A>G	6R	170.4
4201677|F|0-8:T>C-8:T>C	6R	173.4
3609368|F|0-23:A>G-23:A>G	6R	174.1
3608719|F|0-18:A>G-18:A>G	6R	175.4
3043454|F|0-26:T>C-26:T>C	6R	176.8
4564225|F|0-44:G>C-44:G>C	6R	180.1
8512626|F|0-16:G>A-16:G>A	6R	181.7
3617691|F|0-20:A>G-20:A>G	6R	184
8537308|F|0-21:T>C-21:T>C	6R	186.9
3603593|F|0-31:T>C-31:T>C	6R	187
4213219|F|0-56:A>G-56:A>G	6R	189.7
3617968|F|0-44:T>A-44:T>A	6R	191.2
4368843|F|0-25:G>C-25:G>C	6R	192.7
4368843|F|0-58:T>G-58:T>G	6R	193.3
8512323|F|0-7:G>A-7:G>A	6R	194.9
4203562|F|0-8:A>G-8:A>G	6R	199.2
4211363|F|0-23:G>C-23:G>C	6R	201.1
10524492|F|0-63:G>A-63:G>A	6R	203.4
3048140|F|0-16:G>C-16:G>C	6R	206.1
8536991|F|0-14:A>G-14:A>G	6R	208.3
4347252|F|0-20:C>A-20:C>A	6R	208.8
3047025|F|0-61:C>G-61:C>G	7A	0
8510331|F|0-22:C>G-22:C>G	7A	3.6
4216795|F|0-9:G>T-9:G>T	7A	5.7
19758442|F|0-11:C>A-11:C>A	7A	7.7
11912988|F|0-7:G>A-7:G>A	7A	9.5
10521319|F|0-6:A>G-6:A>G	7A	10.1
8509727|F|0-17:C>A-17:C>A	7A	11.3
4214399|F|0-28:T>C-28:T>C	7A	11.3
4566440|F|0-15:G>A-15:G>A	7A	13.6
4210707|F|0-55:C>T-55:C>T	7A	13.9
4358654|F|0-16:A>G-16:A>G	7A	16.7
8512212|F|0-5:T>C-5:T>C	7A	19.2
3043440|F|0-22:G>A-22:G>A	7A	22
19759008|F|0-60:T>C-60:T>C	7A	23.7
8509724|F|0-44:T>C-44:T>C	7A	29.7
4565419|F|0-47:G>T-47:G>T	7A	31.3
8511746|F|0-6:G>A-6:G>A	7A	34.6
4344015|F|0-42:T>C-42:T>C	7A	35.7
8511596|F|0-5:G>A-5:G>A	7A	36.9
10517254|F|0-5:C>T-5:C>T	7A	38.2
4210062|F|0-30:T>A-30:T>A	7A	48.5
3040824|F|0-29:C>G-29:C>G	7A	52.9
4368539|F|0-41:C>A-41:C>A	7A	65.7
4356726|F|0-18:A>C-18:A>C	7A	67.5
3043247|F|0-40:C>T-40:C>T	7A	70.5
8510104|F|0-16:C>T-16:C>T	7A	72
4346295|F|0-22:A>G-22:A>G	7A	86.1

8510339|F|0-25:A>C-25:A>C	7A	89.6
4345289|F|0-18:A>T-18:A>T	7A	92.8
4365444|F|0-17:C>G-17:C>G	7A	96.4
8538497|F|0-5:G>A-5:G>A	7A	98.5
4365701|F|0-33:G>A-33:G>A	7A	100.6
3043390|F|0-46:C>T-46:C>T	7A	103.3
4212270|F|0-11:T>C-11:T>C	7A	108.3
4549474|F|0-30:A>G-30:A>G	7A	108.9
10524688|F|0-21:A>G-21:A>G	7A	110.4
4207133|F|0-7:G>A-7:G>A	7A	112.6
3040859|F|0-10:A>G-10:A>G	7A	113.9
4368103|F|0-61:G>A-61:G>A	7A	117.2
3610348|F|0-12:G>C-12:G>C	7A	121.5
8535359|F|0-35:C>G-35:C>G	7A	123.6
3048180|F|0-6:T>C-6:T>C	7A	128.3
4350450|F|0-11:T>C-11:T>C	7A	130.8
3047348|F|0-9:C>T-9:C>T	7A	132.2
3047410|F|0-56:G>A-56:G>A	7A	133.6
3046683|F|0-21:T>C-21:T>C	7A	136.3
4210132|F|0-27:C>G-27:C>G	7A	138.5
3044607|F|0-8:T>C-8:T>C	7A	139.3
19759127|F|0-20:T>G-20:T>G	7A	140.2
3046716|F|0-33:C>T-33:C>T	7A	141.6
3045484|F|0-39:G>C-39:G>C	7A	142.4
3040817|F|0-66:T>G-66:T>G	7A	146.4
4365299|F|0-18:G>A-18:G>A	7A	148.4
3606651|F|0-14:G>A-14:G>A	7A	150
3619224|F|0-27:G>A-27:G>A	7A	152.5
3621171|F|0-11:T>A-11:T>A	7A	152.7
3617251|F|0-10:G>C-10:G>C	7A	154.8
4564732|F|0-22:C>G-22:C>G	7A	156.8
8510360|F|0-7:G>A-7:G>A	7A	157.6
4366897|F|0-21:A>C-21:A>C	7A	163.4
4216793|F|0-25:G>A-25:G>A	7A	166.6
3041789|F|0-49:C>G-49:C>G	7A	176
4212233|F|0-6:G>A-6:G>A	7A	181.1
3042820|F|0-35:A>C-35:A>C	7A	184
4354035|F|0-14:A>G-14:A>G	7A	187.4
4212761|F|0-44:A>G-44:A>G	7A	198.8
3613527|F|0-27:T>C-27:T>C	7A	199.9
3046262|F|0-53:G>C-53:G>C	7A	202.2
4208214|F|0-52:C>T-52:C>T	7A	203.1
4546240|F|0-7:A>G-7:A>G	7A	203.1
4212702|F|0-52:T>C-52:T>C	7B	0
4365215|F|0-14:A>G-14:A>G	7B	0
4206568|F|0-23:A>G-23:A>G	7B	3.7
4342210|F|0-24:A>G-24:A>G	7B	5.5
4207627|F|0-30:C>G-30:C>G	7B	10.7

3043611|F|0-39:T>C-39:T>C	7B	15.2
8537929|F|0-51:C>T-51:C>T	7B	20.3
4208562|F|0-25:T>A-25:T>A	7B	24.8
4565037|F|0-41:G>T-41:G>T	7B	28.1
4209055|F|0-41:A>G-41:A>G	7B	31
3040602|F|0-5:A>T-5:A>T	7B	31.6
4370538|F|0-6:G>A-6:G>A	7B	33.6
3044676|F|0-48:C>T-48:C>T	7B	35.8
4211185|F|0-45:G>A-45:G>A	7B	38.5
4207094|F|0-35:C>G-35:C>G	7B	43.2
4211277|F|0-38:C>A-38:C>A	7B	47
4349134|F|0-6:C>T-6:C>T	7B	50
3047150|F|0-15:C>G-15:C>G	7B	53
3044326|F|0-9:G>A-9:G>A	7B	54.5
4203283|F|0-36:G>C-36:G>C	7B	56.8
3046360|F|0-46:C>G-46:C>G	7B	59.9
4371098|F|0-23:G>A-23:G>A	7B	62.2
3045087|F|0-53:A>G-53:A>G	7B	65.1
4212658|F|0-13:T>C-13:T>C	7B	66.4
3045930|F|0-32:A>G-32:A>G	7B	69.3
3048059|F|0-14:T>C-14:T>C	7B	72.2
4208037|F|0-6:A>T-6:A>T	7B	73.8
4209309|F|0-34:T>C-34:T>C	7B	75.8
4217981|F|0-5:A>G-5:A>G	7B	77
3048209|F|0-21:T>C-21:T>C	7B	80.1
3046546|F|0-11:T>C-11:T>C	7B	87
3045053|F|0-44:T>G-44:T>G	7B	90.2
3047943|F|0-18:A>G-18:A>G	7B	90.3

(Agostino x Grenado) x G8.06 (AG) population

Marker name	Linkage group	position (cM)
19758573	1A	0
8534950	1A	6.652353332
8538908	1A	10.74503991
8521370	1A	13.54698245
16331172	1A	17.95327699
11911179	1A	23.84355609
3046278|F|0-7:G>A-7:G>A	1B	0
4216702|F|0-26:T>C-26:T>C	1B	11.52643745
8516114	1B	17.28221881
19757402	1B	22.61020959
10523514	1B	26.222259
10516707	1B	32.29106435
3610710|F|0-18:C>A-18:C>A	1R	0
8521495	1R	5.456409003
3623140	1R	8.81380809
19758407|F|0-5:A>G-5:A>G	1R	14.04886971
10523289	1R	19.02765169
16312168|F|0-41:T>C-41:T>C	1R	22.26277555
4362749|F|0-28:G>C-28:G>C	1R	26.52522489
8512333|F|0-9:G>C-9:G>C	1R	31.65420779
4557615	1R	34.7610238
10516642|F|0-14:T>C-14:T>C	1R	36.7846223
4341637|F|0-6:T>C-6:T>C	1R	44.43821652
4370690|F|0-38:C>T-38:C>T	1R	53.54105995
4215623|F|0-8:G>C-8:G>C	1R	65.72658414
4548512	1R	69.98603136
4558656	1R	73.21508209
19758128	1R	79.89229885
4345215|F|0-23:C>A-23:C>A	2A	0
4213666	2A	6.069641321
3616554	2A	7.891076775
4213005|F|0-13:G>T-13:G>T	2A	11.98932653
4212527	2A	15.04397014
4221572	2A	16.74719755
3046836|F|0-36:C>T-36:C>T	2A	23.65190388
4210047|F|0-27:G>A-27:G>A	2A	38.12639768
4372110|F|0-18:C>T-18:C>T	2B	0
4360063	2B	5.154555801
16353677	2B	13.64647968
3046768|F|0-15:A>G-15:A>G	2B	17.94296745
19757199	2B	21.67978473
19757226	2B	24.91496257
14475928|F|0-10:T>A-10:T>A	2B	33.4485594
4348732	2B	42.64832022

10516388	2B	46.96650156
8519870	2B	49.68509124
3610361	2B	53.04633235
3615575|F|0-22:C>G-22:C>G	2B	57.45697382
4208738|F|0-6:A>G-6:A>G	2B	75.01668251
4208900|F|0-67:G>C-67:G>C	2B	85.59385583
10513052	2B	96.88589257
14472468	2B	102.093816
3042052|F|0-5:G>A-5:G>A	2B	105.7164429
8535079	2B	113.1896052
8510541|F|0-15:T>C-15:T>C	2B	120.3129952
3619558	2B	125.1436798
10521024|F|0-13:A>G-13:A>G	2B	128.9896796
3607486|F|0-24:T>G-24:T>G	2B	137.7399181
3622821	2B	143.3593183
3605484|F|0-35:A>C-35:A>C	2B	145.9457782
4563131	2B	149.7049704
4553468|F|0-34:T>G-34:T>G	2B	153.4396524
3042218|F|0-11:A>G-11:A>G	2B	156.9642134
8510350|F|0-18:G>C-18:G>C	2B	164.4076146
3044977|F|0-35:A>C-35:A>C	2B	174.2007465
3040771|F|0-59:T>C-59:T>C	2B	180.5982514
4368097|F|0-60:T>C-60:T>C	2B	185.8425159
4353437|F|0-13:G>A-13:G>A	2B	191.5917076
3046713|F|0-25:C>G-25:C>G	2B	198.7797034
8534980|F|0-7:G>C-7:G>C	2B	204.2472761
3040773|F|0-38:C>T-38:C>T	2B	210.1379624
3624999|F|0-20:T>C-20:T>C	2B	221.2149715
8511413|F|0-34:A>G-34:A>G	2B	238.0459515
4572354	2B	244.8760409
4202838|F|0-28:G>C-28:G>C	2B	249.6202803
14479678|F|0-11:G>A-11:G>A	3A	0
19757700	3A	13.31452755
10503667	3A	16.8198114
4556585	3A	19.27491615
8515245	3A	21.32619552
8532795|F|0-30:T>C-30:T>C	3A	25.51266788
4364793|F|0-13:C>G-13:C>G	3A	37.40365172
8509699|F|0-31:G>C-31:G>C	3A	45.72705121
3040639|F|0-34:G>A-34:G>A	3A	50.6582162
4212987|F|0-11:A>C-11:A>C	3A	54.97628925
14476475	3A	60.76617073
3609296|F|0-24:C>T-24:C>T	3B	0
19757071	3B	8.29493904
3046991|F|0-20:A>G-20:A>G	3B	12.53218424
4560351	3B	17.11054643
8520602	3B	21.73594813
4208877|F|0-37:C>T-37:C>T	3B	26.05010093

SSR_GWM533	3B	38.80328612
10524243|F|0-32:G>A-32:G>A	3B	53.41011509
3604347	5A	39.86218569
Xiac0134	5R	15.02413523
Xiac0132	5R	15.60466691
3619326	5R	17.34022796
Xiac0135	5R	19.78577271
4351948	5R	39.5925535
3044240|F|0-32:T>A-32:T>A	5R	103.5336198
4562694	5R	149.8013215
4205132	5R	154.7922624
19757597	5R	159.4620367
4363849|F|0-45:T>G-45:T>G	5R	223.5184381
3040766|F|0-12:A>C-12:A>C	5R	237.8596615
3042635|F|0-56:G>T-56:G>T	5R	283.6141777
4221573|F|0-11:C>A-11:C>A	5R	338.8861888
10497613	5R	343.6714198
4218892	5R	346.561562
4217596	5R	347.2055444
4213885	5R	348.5402472
10507075	5R	353.0962718
4550259	6B	19.80317967
14479870|F|0-26:A>T-26:A>T	3B	58.48279073
10524972|F|0-56:G>C-56:G>C	3B	61.40004982
4555442|F|0-20:G>A-20:G>A	3B	71.63201961
14479678|F|0-40:G>C-40:G>C	3B	81.40311015
10522275|F|0-14:A>G-14:A>G	3B	87.50122603
4565144|F|0-28:T>G-28:T>G	3B	94.26310678
SSR_GWM493	3B	110.1621323
8539436	3B	119.8586255
11908516	3B	124.1867868
11908503	3B	126.6586431
3612135|F|0-42:T>G-42:T>G	3B	131.5399685
4554401|F|0-12:C>T-12:C>T	3B	141.0369489
3613350|F|0-32:T>C-32:T>C	3B	148.9351749
3623829|F|0-26:T>C-26:T>C	3B	158.5052572
3048012|F|0-48:C>A-48:C>A	3B	186.4461967
14476350|F|0-26:C>G-26:C>G	3B	191.0703418
10525346|F|0-14:A>T-14:A>T	3B	194.4677277
4567314|F|0-58:G>C-58:G>C	3B	203.7991594
14476457	3B	205.9472447
14470335	3B	207.7501567
14468732	3R	0
19758881	3R	7.952417417
10518230	3R	12.20977989
4208183|F|0-39:G>A-39:G>A	3R	16.37707752
4365220|F|0-7:T>C-7:T>C	3R	32.0869382
8512645|F|0-49:G>C-49:G>C	3R	43.55579444

8539707|F|0-12:A>G-12:A>G	3R	49.43661344
4213873	3R	52.91218905
15997458	3R	56.29925338
11908196	3R	60.95794007
4372363	3R	63.02328841
4563779|F|0-22:T>C-22:T>C	3R	66.14181049
4339465	3R	70.58007441
4347109|F|0-24:G>T-24:G>T	3R	73.92572684
8514266	3R	76.61034027
8513620	3R	78.93616462
4553262	3R	83.11640501
8513625	3R	87.26073216
#N/A	4A	0
#N/A	4A	15.39850373
#N/A	4A	64.78194645
#N/A	4A	89.52204717
#N/A	4A	155.2428416
10522958|F|0-15:G>A-15:G>A	4B	0
10500352	4B	2.356419754
10511692	4B	4.801877031
4371444	4B	10.73968589
3606573|F|0-28:G>A-28:G>A	4R	0
19757187	4R	13.10857239
3045043|F|0-23:C>G-23:C>G	4R	20.80587908
19757342	4R	34.03781843
10519603	4R	38.59349453
4561212	4R	42.81599344
4215451	4R	46.53766337
8509686|F|0-25:T>C-25:T>C	4R	49.36294756
4216916	4R	55.39622189
8511594|F|0-10:G>A-10:G>A	4R	64.32068969
3608967	4R	69.07343745
19757775	4R	71.85258358
10504639	4R	72.64280149
8510212|F|0-10:C>T-10:C>T	4R	74.095852
19758669|F|0-16:G>C-16:G>C	4R	78.74037162
10522862	4R	81.06236297
10504950	4R	84.79082186
4359518|F|0-16:G>T-16:G>T	4R	88.19476169
8517171	4R	90.34321606
19759140	4R	92.19076101
19757149	4R	94.39388512
4217850	4R	96.59609671
8511227|F|0-21:A>C-21:A>C	4R	103.1332636
8531509|F|0-25:G>C-25:G>C	4R	110.5826699
3618968|F|0-59:G>A-59:G>A	4R	119.1059251
3613208|F|0-18:A>G-18:A>G	4R	128.7436731
3620154|F|0-36:C>A-36:C>A	4R	138.6351384

3048042|F|0-28:C>G-28:C>G	4R	154.024517
19757038	3B	211.5586244
11908446	3B	215.6974957
3621749	3B	220.9670944
4200724	3B	224.6357308
3616847|F|0-47:G>T-47:G>T	3B	238.3614621
3613664|F|0-16:A>C-16:A>C	3B	248.1171095
4353853|F|0-14:A>G-14:A>G	3B	254.0569629
4214553	3B	257.9830878
4214040	3B	259.5239443
10518808	3B	261.3165687
10523888|F|0-9:T>C-9:T>C	3B	265.1682483
4204778	3B	268.9537176
4217649	3B	272.5270961
4217378	3B	277.6292162
4203391	3B	280.3074822
8512797|F|0-16:A>G-16:A>G	3B	289.7067158
3613038|F|0-26:T>C-26:T>C	3B	303.7359933
4221332|F|0-23:C>T-23:C>T	3B	320.1424849
8521580	3B	326.0568194
8510700	3B	348.177684
4342838|F|0-43:C>T-43:C>T	5A	0
3046729|F|0-33:T>G-33:T>G	5A	8.782239919
3615965	5A	14.63619583
3622467|F|0-60:C>T-60:C>T	5A	19.89595432
8521652	5A	24.63184024
3043362|F|0-33:G>A-33:G>A	5A	31.36018471
3619312|F|0-12:G>C-12:G>C	5A	37.1073129
8534109	5A	44.41262779
3041308|F|0-25:C>T-25:C>T	5A	51.3447167
4367859|F|0-39:T>C-39:T>C	5B	0
10519984	5B	6.333492751
10496303	5B	9.848186263
4339697	5B	13.00974995
4341664	5B	18.56198415
4369117	5B	20.85670466
3609739	5B	25.92015036
3605462|F|0-31:C>G-31:C>G	5B	29.16276054
4349704|F|0-63:C>T-63:C>T	5B	34.28316806
4348234|F|0-5:C>G-5:C>G	5B	38.84940016
4551070|F|0-15:G>C-15:G>C	5B	43.97032215
3616958|F|0-25:C>T-25:C>T	5B	49.0747637
3048005|F|0-57:G>A-57:G>A	5B	52.6396129
4346347|F|0-38:G>C-38:G>C	5B	57.45990666
3617366|F|0-14:T>C-14:T>C	5B	64.24707446
8511684|F|0-25:G>A-25:G>A	5B	71.77943176
8515404	5B	82.93227689
3612609	5B	90.44214414

4544823	5B	98.95456861
4339703	5B	100.7323923
4547304	5B	104.0766185
3610616|F|0-46:A>G-46:A>G	5B	111.876385
8513201	5B	120.1524568
3604438|F|0-5:A>G-5:A>G	5B	130.5808874
8519965	5B	133.3074981
4216474	5B	135.8298945
4349657|F|0-17:G>A-17:G>A	5A	60.29155822
4358724|F|0-28:C>A-28:C>A	5A	70.24708111
3616918|F|0-7:C>G-7:C>G	5A	77.58369097
4219458	5A	81.85039748
4368950|F|0-35:C>G-35:C>G	5A	87.5257757
4361203|F|0-42:G>T-42:G>T	5A	95.75260805
3042383|F|0-68:C>A-68:C>A	5A	106.2087639
3613518	5A	111.978656
4360918	5A	114.2065369
4368543|F|0-12:T>C-12:T>C	5A	124.3543021
3043439|F|0-42:A>C-42:A>C	5A	132.180963
4346745	5A	137.7631292
4219794	5A	140.6365456
4368313|F|0-58:T>G-58:T>G	5A	145.9733158
8536847|F|0-31:C>G-31:C>G	5A	154.582547
4349070|F|0-19:A>G-19:A>G	5A	161.0491316
3041628|F|0-34:A>G-34:A>G	5A	167.1718982
3047420|F|0-46:T>C-46:T>C	5A	173.9207237
10497551	5A	179.1002318
3046128|F|0-28:C>G-28:C>G	5R	0
4352888	5R	12.72816617
Xiac0131	5R	16.18807192
Xiac0130	5R	18.55484192
Xiac0129	5R	19.16897423
4358629	5R	31.75372796
3045841|F|0-29:A>G-29:A>G	5R	37.14103388
4213124	5R	41.45535678
8537234|F|0-28:A>C-28:A>C	5R	48.44752912
4354271|F|0-37:G>C-37:G>C	5R	54.69624659
4213814|F|0-24:A>T-24:A>T	5R	63.22332815
8510162|F|0-40:C>T-40:C>T	5R	72.02157144
8535029|F|0-17:T>A-17:T>A	5R	79.47036834
8511883|F|0-37:C>T-37:C>T	5R	85.66831522
4218144|F|0-24:T>C-24:T>C	5R	93.49215548
3041777|F|0-14:C>A-14:C>A	5R	97.75340397
4339199	5R	106.1687845
8514998	5R	110.4496391
19758131	5R	134.1778379
10494680	5R	145.6651342
8537997	5R	151.236454

4575335	5R	156.6277286
4356752|F|0-8:G>T-8:G>T	5R	165.5686227
3046746|F|0-36:A>G-36:A>G	5R	173.2490192
8531860|F|0-9:G>A-9:G>A	5R	179.8949307
4207009|F|0-30:T>C-30:T>C	5R	189.2029838
4351372|F|0-29:T>C-29:T>C	5R	196.2673528
4571646|F|0-6:A>C-6:A>C	5R	202.2760754
8537532|F|0-8:A>G-8:A>G	5R	207.9875291
3607876|F|0-46:T>C-46:T>C	5R	215.6114741
4368663|F|0-8:C>T-8:C>T	5R	220.2572504
4566050|F|0-55:G>C-55:G>C	5R	228.6139872
4209185	5R	233.4065861
3042131	5R	240.238945
4358973|F|0-14:T>C-14:T>C	5R	245.7183188
10521923|F|0-28:C>G-28:C>G	5R	253.1013717
4343052|F|0-32:T>C-32:T>C	5R	260.2530523
4372663|F|0-19:C>T-19:C>T	5R	266.4340309
3623312|F|0-68:T>C-68:T>C	5R	272.9157898
3622590|F|0-19:T>C-19:T>C	5R	279.0570157
3622843|F|0-45:G>C-45:G>C	5R	289.8408274
4221592|F|0-20:G>C-20:G>C	5R	295.1649707
10524133|F|0-14:A>G-14:A>G	5R	300.0466679
4204938|F|0-37:C>T-37:C>T	5R	305.8624269
4218228|F|0-10:C>A-10:C>A	5R	314.0563524
3044550|F|0-17:A>G-17:A>G	5R	320.2669771
4201323|F|0-11:T>G-11:T>G	5R	327.4740906
10510650	5R	331.9503362
3613416|F|0-6:T>A-6:T>A	5R	335.3515645
10509118	5R	341.7601493
4212656|F|0-33:G>A-33:G>A	5R	345.2739902
4203306	5R	350.14975
3044473|F|0-8:T>C-8:T>C	6A	0
3048122|F|0-15:T>C-15:T>C	6A	12.60195204
4563504|F|0-35:C>A-35:C>A	6A	24.52468999
10521577|F|0-13:G>A-13:G>A	6A	34.40474273
3042853|F|0-55:A>G-55:A>G	6A	42.65331978
3045975|F|0-13:T>A-13:T>A	6A	49.54978684
19759364	6A	54.89226796
19757664	6A	58.97540737
3041137|F|0-13:C>A-13:C>A	6A	71.09532277
4365034	6A	80.57187313
4573562|F|0-62:G>A-62:G>A	6A	86.80059106
3623503	6A	93.11398744
4573024|F|0-7:C>A-7:C>A	6A	97.75146765
3623881	6A	101.4393029
16356066	6A	104.8586385
3605216|F|0-45:C>G-45:C>G	5R	361.2140145
4575464|F|0-10:C>A-10:C>A	6B	0

19759462	6B	5.659374148
4359637|F|0-33:T>C-33:T>C	6B	10.99077272
3621401|F|0-56:T>C-56:T>C	6B	16.8110463
4203605	6B	21.36093726
4552045	6B	24.03197578
10500172	6B	42.93501765
10522217|F|0-19:C>G-19:C>G	6R	0
19759141|F|0-8:C>T-8:C>T	6R	20.80941473
4204096|F|0-6:A>G-6:A>G	6R	27.26428582
4573888|F|0-46:A>G-46:A>G	6R	34.54115991
4555297	6R	39.11068117
3045613|F|0-5:T>C-5:T>C	6R	43.72890204
3613238|F|0-8:C>G-8:C>G	6R	56.68444777
4545735|F|0-7:T>G-7:T>G	6R	64.3977888
10520166	6R	70.24443881
4211453|F|0-6:G>C-6:G>C	6R	79.17851638
19759143	6R	83.87962104
4551684	6R	88.75126376
10522910	6R	93.54386267
4211242|F|0-38:G>T-38:G>T	6R	96.66454981
3046607|F|0-22:G>C-22:G>C	6R	105.050548
3618027	6R	107.7760502
3623183	6R	109.8030902
3621978	6R	112.3918203
3624101|F|0-18:T>A-18:T>A	6R	115.6476538
4207478|F|0-27:T>G-27:T>G	6R	124.1012171
3043630|F|0-26:A>G-26:A>G	6R	135.2318288
10521673|F|0-59:C>A-59:C>A	6R	146.4459089
3043785|F|0-15:C>A-15:C>A	6R	155.0118731
3046672|F|0-37:A>G-37:A>G	6R	161.845893
16358693|F|0-11:G>A-11:G>A	6R	167.5364756
16328747	6R	172.859928
19757820	6R	180.4668264
4575453|F|0-46:T>C-46:T>C	7A	0
4346295|F|0-22:A>G-22:A>G	7A	15.43981079
3045662|F|0-37:A>C-37:A>C	7A	24.15980854
10524688|F|0-21:A>G-21:A>G	7A	31.9945755
4212270|F|0-11:T>C-11:T>C	7A	38.87415588
4366491	7A	43.68115957
3044826|F|0-60:A>G-60:A>G	7A	48.56563595
3040781|F|0-29:C>T-29:C>T	7A	54.98283758
3041321|F|0-63:A>G-63:A>G	7A	62.62435201
3042384|F|0-16:C>A-16:C>A	7A	71.94699912
10499198	7A	75.45177135
3620501|F|0-51:T>C-51:T>C	7A	80.69592715
3047209|F|0-25:C>T-25:C>T	7A	88.84294323
3045621|F|0-68:A>G-68:A>G	7A	93.19048574
8510968|F|0-15:C>T-15:C>T	7A	99.18035327

3044254|F|0-49:T>C-49:T>C	7A	108.772005
15996448	7A	113.6230259
4574603	7A	119.1955691
10511579	7A	121.6606243
3046073|F|0-6:T>C-6:T>C	7A	124.5774804
4552728	7A	129.1311572
3044607|F|0-8:T>C-8:T>C	7A	132.4401379
4210132|F|0-27:C>G-27:C>G	7A	140.908821
3040817|F|0-66:T>G-66:T>G	7A	152.0568956
10498027	7A	156.7550811
3606651|F|0-14:G>A-14:G>A	7A	161.5580491
4564732|F|0-22:C>G-22:C>G	7A	173.6235214
10507598	7A	180.3056472
4217780	7A	189.8179846
3621489|F|0-54:A>C-54:A>C	7B	0
4370908|F|0-41:T>G-41:T>G	7B	12.72193895
4570308	7B	21.28257975
10516838|F|0-30:C>A-30:C>A	7B	25.54314021
3047237|F|0-6:G>C-6:G>C	7B	32.24883106
3047943|F|0-18:A>G-18:A>G	7B	36.54726209
3610037|F|0-5:C>G-5:C>G	7B	41.92745331
8511444|F|0-55:T>C-55:T>C	7B	45.52541781
4207533|F|0-19:T>C-19:T>C	7B	51.83316593
3622544|F|0-25:C>T-25:C>T	7B	64.92621929
4204460|F|0-27:A>C-27:A>C	7B	89.47528627
4557077	7B	93.1931309
3046159|F|0-17:G>C-17:G>C	7B	94.9395096
4345380	7B	98.4508711
4574038|F|0-39:A>C-39:A>C	7B	107.0603368
4547712|F|0-44:C>T-44:C>T	7B	120.2863542
4342210|F|0-24:A>G-24:A>G	7B	131.7235883
4213407	7B	134.0923795
4365432	7B	138.3189057
8522426	7B	142.9835175
8522492	7B	147.1811867
4221374	7B	152.4368142
4372883	7B	158.2353169
8517452	7B	167.831387
4351197	7B	170.8151786
11909959	7B	177.2180484
3042323|F|0-56:G>A-56:G>A	7B	183.8052016
4373565|F|0-65:G>C-65:G>C	7B	193.4173701
4356232|F|0-28:G>A-28:G>A	7B	198.8127459
4366408	7B	201.418091
4548722	7B	203.2187026
3618274|F|0-27:T>C-27:T>C	7B	206.5454906
3623602	7B	208.5354724
3609507|F|0-44:C>T-44:C>T	7B	213.0542496

3621128	7B	215.9385722
8513043	7B	218.8926417
3616215|F|0-10:A>G-10:A>G	7B	223.872377
3619185|F|0-30:A>G-30:A>G	7B	231.6738315

El Paso x G8.06 (E) population

Marker name	Linkage group	position (cM)
4214595	1A	0
4363282|F|0-62:A>G-62:A>G	1A	17.15226101
19759345|F|0-26:G>A-26:G>A	1A	26.17388808
8515420	1A	28.70555405
4367734|F|0-68:A>G-68:A>G	1A	36.97838311
4214295|F|0-32:T>C-32:T>C	1A	55.255346
10497934	1A	81.96524028
4203826	1A	96.21112765
4550610	1A	99.66105107
3046858|F|0-36:A>G-36:A>G	1A	105.6756658
4204236|F|0-46:C>A-46:C>A	1A	129.4902211
4204543	1A	148.9485838
4352491	1B	0
4353345	1B	29.62068263
4343462	1B	43.17979998
3048085|F|0-36:T>G-36:T>G	1B	56.62552674
4340171|F|0-39:A>G-39:A>G	1B	74.43358209
4209147|F|0-33:C>A-33:C>A	1B	87.24197805
4562175	1B	94.63544374
4358048	1B	101.9229033
3045148|F|0-31:G>A-31:G>A	1B	111.402599
4549161	1B	127.7190328
8511311|F|0-7:C>T-7:C>T	1B	138.6384726
3605115	1B	154.0014894
3606457	1B	158.5507604
8513421	1B	162.4733719
4349685	1B	174.2858098
4569232	1B	183.4534234
4569556	1B	192.8207849
11909214	1B	206.681112
4215139	1B	217.3273108
4564233|F|0-7:A>G-7:A>G	1B	233.3358084
4369535	1R	0
4373891|F|0-32:T>C-32:T>C	1R	11.16488164
10519563	1R	17.26187092
11909798	1R	20.30225183

4345101	1R	25.22555646
8521667	1R	30.62553179
4217527	1R	34.78811556
10523666	1R	42.94314492
3613167	1R	50.8576542
3043064	1R	60.10722938
4550098	1R	65.05213361
8538984	1R	70.31409045
4345387	1R	79.96597807
4214759	1R	83.71371483
4358076|F|0-7:T>C-7:T>C	1R	89.70641763
3612768	1R	96.98216529
10523462|F|0-10:T>C-10:T>C	1R	103.2188918
15996853	1R	111.0691651
4362749|F|0-28:G>C-28:G>C	1R	117.2552334
3606480	1R	122.944145
8517600	1R	134.7895716
4557531	2A	0
8510930|F|0-56:T>A-56:T>A	2A	29.57467716
3044210|F|0-64:T>C-64:T>C	2A	44.85230979
3047543|F|0-30:A>G-30:A>G	2A	57.6933981
8512004	2A	65.61181421
3042841|F|0-25:G>A-25:G>A	2A	74.38163279
8521400	2A	83.33360088
4566673	2A	92.48645166
4344011	2A	108.1835582
3619025	2B	0
3608484|F|0-29:C>T-29:C>T	2B	32.06937588
3042052|F|0-5:G>A-5:G>A	2B	54.25346013
8519697	2B	68.49259825
3614728|F|0-45:C>G-45:C>G	2B	78.63881145
10517207|F|0-9:A>G-9:A>G	2B	91.03092583
3612327|F|0-46:C>G-46:C>G	2B	106.255191
4549207	2B	117.606915
4342516|F|0-20:G>T-20:G>T	2B	123.4497156
3040807|F|0-48:A>T-48:A>T	2B	140.2493614
19759231	2B	148.6013889
19758341	2B	155.6978633
19757302	2B	166.456429
3604711	2B	178.8271029
19758198	2B	189.0792151
4340308	2R	0
3615081	2R	6.611336279
4360764	2R	13.71757783
10517057	2R	25.11598535
4359798	3A	0
4566342	3A	8.070823865
3041254|F|0-56:A>G-56:A>G	3A	22.22476741

3042146|F|0-58:G>A-58:G>A	3A	33.80262315
4360245|F|0-11:A>T-11:A>T	3A	45.90753472
4361922	3A	60.19974463
4370707|F|0-21:C>T-21:C>T	3A	73.84417823
GWM533	3B	0
8539436|F|0-7:C>T-7:C>T	3B	16.70172377
GWM493	3B	34.1200653
3619105	3B	59.56825332
8519659	3B	79.39556077
4218906	3B	94.92927335
8519238	3B	103.0818256
4553952	3B	110.6849343
3046639	3B	115.0590972
4344110	3B	125.3892322
4367239|F|0-38:A>G-38:A>G	3B	137.0505668
4201477	3B	159.4404641
4348225	4A	0
11911648	4A	14.23204495
8522806	4A	25.12106556
10521701|F|0-7:C>G-7:C>G	4A	36.71577593
11912700|F|0-26:C>G-26:C>G	4A	47.46491207
4340035	4A	51.24590412
4370293|F|0-6:C>T-6:C>T	4A	58.6566019
4370293|F|0-24:G>C-24:G>C	4A	63.20807134
4356251	4A	69.69734207
3041350|F|0-53:T>C-53:T>C	4A	74.47550975
10497209	4A	82.99545298
10524876|F|0-5:A>C-5:A>C	4A	89.11910769
4346262	4A	95.85380514
4365305	4A	100.9557713
14473755	4A	111.4040067
10514293	4A	130.3001161
14477891|F|0-14:A>G-14:A>G	4A	154.8534123
3614122	4B	0
4221434	4B	15.81170225
4204523	4B	29.99873936
4550060	4R	0
4355728|F|0-41:T>A-41:T>A	4R	23.13837853
4356250|F|0-7:G>C-7:G>C	4R	37.69026899
8517639	4R	45.69424832
4366861|F|0-27:A>G-27:A>G	4R	50.9268929
10512136|F|0-6:T>C-6:T>C	4R	65.37471941
3611647	4R	73.8739839
10521823	4R	76.58502008
3613362	4R	78.99990086
3621477	4R	81.32703186
4367165|F|0-46:A>C-46:A>C	4R	84.511339
19758495|F|0-16:A>G-16:A>G	4R	92.4446148

4368029|F|0-33:T>C-33:T>C	4R	101.4540745
8513490	4R	108.6525509
8511126	4R	113.0523787
4367528|F|0-35:G>C-35:G>C	4R	117.7521415
3041453|F|0-39:G>T-39:G>T	4R	124.0591747
8514049	4R	127.6475107
4564471|F|0-20:T>G-20:T>G	4R	135.2173715
3616653|F|0-58:C>G-58:C>G	4R	150.0717271
3615005|F|0-55:T>C-55:T>C	4R	168.1856806
3615005|F|0-49:A>C-49:A>C	4R	173.7133658
4203199	4R	185.3557849
8509973|F|0-17:A>G-17:A>G	4R	191.3610031
3614918|F|0-23:A>C-23:A>C	4R	203.7775907
4352918	4R	214.2611819
8511474|F|0-65:T>A-65:T>A	4R	225.6729956
4213030	5A	0
4202891	5A	13.02299548
4341743	5A	26.44805873
4348570|F|0-62:T>G-62:T>G	5A	32.49819987
3040691|F|0-52:C>A-52:C>A	5A	52.07069613
8512997|F|0-15:G>C-15:G>C	5A	61.08841643
11909867	5A	66.81973057
8515505	5A	70.18966717
8515141	5A	77.38086048
19758088	5A	85.69477785
3612414	5A	92.65356428
3622319	5A	100.600531
11909166	5A	108.8684958
8522752	5A	116.8179286
4340349	5A	127.7699636
4343261	5A	130.6918321
4561479	5A	135.1486914
8513836	5A	139.3289569
3046809	5A	142.2760407
4560631	5A	154.469686
3041551|F|0-68:G>T-68:G>T	5A	169.3082827
3042912|F|0-22:C>T-22:C>T	5A	206.0119311
4339476	5A	213.1978189
3620835	5A	220.9871142
4547921	5A	234.6805362
4552376	5A	238.1086487
3620113	5A	241.1950915
8517179	5A	246.0773092
19758089	5A	251.7043432
4559414	5A	261.3416298
3617012|F|0-24:G>C-24:G>C	5A	276.2575321
4205525	5A	284.9211187
B180	5A	297.0488269

B56	5A	317.6690196
3609959	5A	328.0974126
4213869	5A	335.829077
4358304|F|0-13:T>G-13:T>G	5A	344.9483069
8518040	5A	367.9321986
3044451|F|0-13:A>G-13:A>G	5A	380.274583
3044668|F|0-23:G>T-23:G>T	5A	396.9391776
3607354	5B	0
4570425	5B	25.07564658
4218856	5B	46.37093841
8517390	5B	62.28327011
4545103	5B	72.01309103
3621999	5B	77.08826286
3614451	5B	82.3244695
4203410	5B	86.88829926
8514774	5B	91.09495283
8533459	5B	93.20806365
11908420	5B	97.33797778
4373782	5B	103.6583305
4217701	5B	108.6399813
8516835	5B	111.1142949
8510510	5B	113.2791213
4341347	5B	118.3747121
4371108|F|0-24:A>G-24:A>G	5B	137.6963353
10514814|F|0-21:A>G-21:A>G	5B	153.1993481
4369389|F|0-6:G>A-6:G>A	5B	163.6018973
10514255|F|0-33:G>T-33:G>T	5B	172.5884016
3613141	5B	183.5994978
10495732	5B	190.7655114
4216748	5B	201.5213917
4339619	5B	213.7869674
4364903	5B	224.404648
4201091	5B	231.99989
4347049|F|0-19:A>G-19:A>G	5B	238.8569613
4555660	5B	254.5735655
11912744	5B	289.1678672
3622440	5B	312.8627124
4355792|F|0-27:C>T-27:C>T	5B	332.3401667
4351717	5B	345.618943
4552808	5B	359.1207175
4367859|F|0-39:T>C-39:T>C	5B	372.600817
4204538	5B	390.103108
10524936|F|0-22:A>G-22:A>G	5B	404.0541425
4552432	5B	415.8563038
4544998	5B	421.905531
3604930	5B	426.8076554
3605189	5B	433.0167532
4203880	5B	441.2471167

4212897	5B	463.9681067
8539573|F|0-62:G>A-62:G>A	5B	479.2842138
10523685|F|0-11:T>C-11:T>C	5B	491.7907207
8509782|F|0-60:C>G-60:C>G	5B	502.4496259
3045122|F|0-8:C>T-8:C>T	5B	518.7205344
4216635|F|0-10:T>C-10:T>C	5B	528.9014339
4210840	5B	545.0303031
4551511	5B	575.0264032
4350011	5B	601.6427582
3621677	5R	0
19759197	5R	17.48477713
4217803|F|0-32:A>G-32:A>G	5R	36.11618384
8531089	5R	43.94068009
10498259	5R	69.80525464
10511640	5R	92.09071592
4368984|F|0-41:G>A-41:G>A	5R	99.51948939
3613806	5R	113.5721757
8510861|F|0-8:C>G-8:C>G	5R	121.992134
3614221|F|0-5:A>G-5:A>G	5R	131.8269045
4355950|F|0-17:A>C-17:A>C	5R	141.3770754
3040999	5R	146.0210483
3613671|F|0-61:T>C-61:T>C	5R	152.2093199
3618115|F|0-24:G>C-24:G>C	5R	161.2197892
4367516|F|0-13:C>G-13:C>G	5R	171.3317271
10508623|F|0-54:G>A-54:G>A	5R	180.2861953
3613715|F|0-10:T>A-10:T>A	5R	190.1159742
3619923|F|0-47:G>A-47:G>A	5R	202.9797672
10520222|F|0-9:C>T-9:C>T	5R	216.3743996
10524840	5R	236.8661832
3615061|F|0-44:C>T-44:C>T	6A	0
3603268	6A	17.71644583
3621599	6A	27.07076005
15998011	6A	35.17680073
4365042	6A	38.70891822
4212965|F|0-64:G>A-64:G>A	6A	49.06360176
4346382|F|0-24:C>T-24:C>T	6A	66.55826953
3608240	6A	82.86266663
3047173|F|0-65:G>A-65:G>A	6A	95.64799264
4574789	6A	101.2492834
4554349	6A	103.9786634
4220364	6A	109.2070894
8510976|F|0-15:G>A-15:G>A	6A	115.3901035
3616261|F|0-30:T>C-30:T>C	6A	124.9781203
4365325	6A	136.3358719
3608860	6A	153.9564155
8519159	6A	160.0663783
3625053	6A	186.5444717
10516559	6A	196.3959769

19757985	6A	206.9275641
19757664	6A	216.3389011
19759364	6A	220.5214047
15996615	6A	225.7161011
19757969	6A	231.3002914
14474739	6A	238.30306
4370194|F|0-6:C>T-6:C>T	6A	246.6386841
19757119	6A	258.7986792
10503572	6A	267.8187618
4573024|F|0-7:C>A-7:C>A	6A	279.4875303
3620295	6A	286.580089
4556562	6A	290.8982991
3046498	6A	296.2411308
8509845	6A	303.8840893
4219305	6A	310.8766406
4363808	6A	314.6545577
4573562|F|0-62:G>A-62:G>A	6A	323.8148794
3613606	6A	346.2066745
4366011	6A	359.6487869
8534067	6A	368.6803842
3603807	6A	384.4057816
4339386	6A	410.695741
4212425	6A	427.286685
4341589|F|0-11:G>A-11:G>A	6A	449.1623415
4340445	6B	0
3040572|F|0-6:A>T-6:A>T	6B	22.14157596
4210067|F|0-29:A>G-29:A>G	6B	37.19114825
4552077	6B	47.48867406
3044730|F|0-11:G>A-11:G>A	6B	52.70235401
4220255|F|0-36:T>G-36:T>G	6B	76.30663611
4349737|F|0-18:A>C-18:A>C	6B	89.64905137
4369576|F|0-15:G>T-15:G>T	6B	97.73839683
4206077|F|0-6:C>T-6:C>T	6B	107.9200591
4202016	6B	120.3825052
4354176	6B	151.1056497
8512302|F|0-65:T>C-65:T>C	6B	165.435536
8514529	6B	176.3958201
10516780	6B	184.9662822
10519200	6B	194.906843
4350272|F|0-25:C>G-25:C>G	6B	214.1735991
4348309	6R	0
4201677|F|0-8:T>C-8:T>C	6R	25.97042943
4573358	6R	40.59858488
3622975	6R	46.61795365
3612362	6R	49.93149776
4571720	6R	53.94090779
4200703	6R	60.02636834
3609911	6R	68.2195328

8535090	6R	74.08844722
8511643	6R	77.93816147
4558863	6R	81.07868084
4353674	6R	86.57518616
3620672	6R	92.23798286
10523766|F|0-66:A>G-66:A>G	6R	98.72130363
4571930	6R	103.4027093
4572592	6R	107.7409341
4200876	6R	113.6342318
8536166	6R	119.2257503
8512338	6R	128.5310406
3611799	6R	136.2646194
3614925	6R	141.0630447
4571382	6R	149.1339839
8512634	6R	152.1429064
4364582	6R	157.2649988
4550470	6R	164.1906093
8515608	6R	171.7353144
4373944	6R	180.1718771
3620271	6R	191.5414131
3604197	6R	201.978447
3606916	6R	204.6140569
8531661|F|0-26:T>G-26:T>G	6R	211.7282486
4205237	6R	220.5287612
4558311	6R	225.322959
10523295	6R	229.4244468
8535154	6R	233.1220029
15997932|F|0-56:C>A-56:C>A	6R	239.8735968
4555495	6R	246.041487
3611483|F|0-61:C>G-61:C>G	6R	251.391154
3611483|F|0-64:A>C-64:A>C	6R	259.8593102
4339800	6R	269.9171168
4211453|F|0-6:G>C-6:G>C	6R	282.7718137
4218572	6R	290.1439515
8534834	6R	294.8938417
8539439	6R	298.0490119
4211775	6R	301.6947271
4209661|F|0-57:G>A-57:G>A	6R	305.3169348
8517274	6R	312.353812
8537923|F|0-23:G>T-23:G>T	6R	324.1915356
4349563|F|0-27:T>C-27:T>C	6R	330.8524701
4342618	6R	342.8187371
4344253	6R	348.4797377
10499175	6R	354.6142593
10500144	6R	362.0043559
4218378	6R	373.817646
4202655	6R	377.451292
10525150|F|0-31:T>C-31:T>C	6R	381.742493

8515412	6R	386.4808812
8510693|F|0-6:T>A-6:T>A	6R	396.4454791
11912933|F|0-24:C>T-24:C>T	6R	407.5551442
4357206	6R	415.4906668
10517507|F|0-20:G>T-20:G>T	6R	424.8905423
4557681	6R	437.5018016
8512066|F|0-41:G>C-41:G>C	6R	444.3260899
4214984	6R	453.051294
4201005	6R	458.3268174
8519690	6R	461.7728894
3047697|F|0-26:C>G-26:C>G	6R	471.5641717
8513697	6R	479.269896
3044986|F|0-33:C>T-33:C>T	6R	490.7451984
3606211	7A	0
14475931	7A	30.11835369
4203084	7A	60.46464752
3622597	7A	77.54300406
4344017	7A	86.2710018
8538562	7A	90.12184612
4341021	7A	94.30020682
10501499	7A	102.808526
3046877|F|0-43:T>C-43:T>C	7A	117.7787108
3613812	7A	128.1326431
8531953	7A	130.3472567
3606377	7A	135.6790513
3048200|F|0-53:G>C-53:G>C	7A	143.932995
3616223	7A	150.2474771
19757727	7A	154.4968426
4205823	7A	161.4367234
8514068	7A	169.9619114
8537041|F|0-44:T>C-44:T>C	7A	182.8903229
11908507	7A	193.4903489
3043275|F|0-11:T>C-11:T>C	7A	209.131948
4217105	7A	222.5838534
3612785	7A	233.0115962
4357889	7A	237.5115255
8521051	7A	240.0104501
4210643|F|0-29:A>G-29:A>G	7A	243.4463707
19759597|F|0-9:C>T-9:C>T	7A	265.6340398
11908235	7A	298.4243688
15998274	7A	324.3148151
4203633	7B	0
4211263|F|0-59:C>T-59:C>T	7B	14.09152562
3046546|F|0-11:T>C-11:T>C	7B	27.31662131
4570308	7B	34.96056904
4347937|F|0-66:G>C-66:G>C	7B	38.19279539
16312545	7B	42.53073492
8521384	7B	44.75884136

4546926	7B	48.38699355
4215654|F|0-34:G>A-34:G>A	7B	54.05217728
15998265	7B	65.00023992
4207094|F|0-35:C>G-35:C>G	7B	77.36255402
4201438|F|0-41:C>G-41:C>G	7B	90.62933026
4210441	7B	100.8477114
4211660|F|0-42:C>T-42:C>T	7B	113.255406
3045131	7B	126.655354

Consensus (T, AG, E) populations

Marker name	Linkage group	position (cM)
4372110|F|0-18:C>T-18:C>T	2B	0
4220071|F|0-12:C>G-12:C>G	2B	3.4
3603506|F|0-15:G>A-15:G>A	2B	3.4
3043964|F|0-31:G>C-31:G>C	2B	4.6
16353188|F|0-39:G>C-39:G>C	2B	7.9
3042109|F|0-23:T>C-23:T>C	2B	29.4
3614695|F|0-40:T>C-40:T>C	2B	34.4
3615575|F|0-22:C>G-22:C>G	2B	37.6
3046768|F|0-15:A>G-15:A>G	2B	38.2
3043752|F|0-16:C>A-16:C>A	2B	42.1
3043472|F|0-42:A>G-42:A>G	2B	42.1
4342979|F|0-18:C>T-18:C>T	2B	42.1
4349371|F|0-17:T>A-17:T>A	2B	42.1
3615895|F|0-39:A>T-39:A>T	2B	44.3
8537224|F|0-10:C>G-10:C>G	2B	44.3
14475928|F|0-10:T>A-10:T>A	2B	44.3
3614728|F|0-45:C>G-45:C>G	2B	53.3
4214570|F|0-65:C>T-65:C>T	2B	54.3
3046048|F|0-33:G>T-33:G>T	2B	54.9
3047224|F|0-46:G>T-46:G>T	2B	62.5
4362126|F|0-24:A>G-24:A>G	2B	65.6
10517207|F|0-9:A>G-9:A>G	2B	67.2
3612327|F|0-46:C>G-46:C>G	2B	84.8
4342516|F|0-20:G>T-20:G>T	2B	103.6
3040807|F|0-48:A>T-48:A>T	2B	123.4
3608484|F|0-29:C>T-29:C>T	2B	127
19759458|F|0-24:T>A-24:T>A	2B	132.7
8513008|F|0-34:G>A-34:G>A	2B	132.7
4568497|F|0-17:C>T-17:C>T	2B	134.1
4552964|F|0-34:T>C-34:T>C	2B	134.1
4207127|F|0-36:G>A-36:G>A	2B	134.8
4557511|F|0-6:A>G-6:A>G	2B	134.9
3048113|F|0-32:T>G-32:T>G	2B	136.3
3607486|F|0-24:T>G-24:T>G	2B	139
4372487|F|0-26:T>G-26:T>G	2B	142.7

10517361|F|0-33:T>C-33:T>C	2B	144
3048234|F|0-31:T>C-31:T>C	2B	144.8
3041167|F|0-65:G>T-65:G>T	2B	147.1
3046194|F|0-31:A>G-31:A>G	2B	147.8
3042042|F|0-5:T>A-5:T>A	2B	149.1
11911490|F|0-41:G>T-41:G>T	2B	149.7
11911705|F|0-32:A>G-32:A>G	2B	150.4
3624999|F|0-20:T>C-20:T>C	2B	151.4
3046713|F|0-25:C>G-25:C>G	2B	153.5
8510541|F|0-15:T>C-15:T>C	2B	153.6
3042052|F|0-5:G>A-5:G>A	2B	153.6
4208900|F|0-67:G>C-67:G>C	2B	153.6
3044946|F|0-19:T>A-19:T>A	2B	158
4573304|F|0-20:A>G-20:A>G	2B	159.3
4568188|F|0-23:G>A-23:G>A	2B	160.8
10520941|F|0-30:T>C-30:T>C	2B	160.8
3040777|F|0-12:G>A-12:G>A	2B	160.8
3042051|F|0-66:G>T-66:G>T	2B	160.8
11912465|F|0-29:A>T-29:A>T	2B	160.8
3048019|F|0-8:C>T-8:C>T	2B	160.8
8511413|F|0-34:A>G-34:A>G	2B	160.8
8534980|F|0-7:G>C-7:G>C	2B	160.8
8511872|F|0-42:C>G-42:C>G	2B	160.8
4202838|F|0-28:G>C-28:G>C	2B	160.8
4353437|F|0-13:G>A-13:G>A	2B	161.1
4368097|F|0-60:T>C-60:T>C	2B	161.1
4561430|F|0-32:C>G-32:C>G	2B	161.9
4210507|F|0-17:G>A-17:G>A	2B	161.9
3043255|F|0-41:G>A-41:G>A	2B	161.9
4210752|F|0-5:C>G-5:C>G	2B	161.9
3042218|F|0-11:A>G-11:A>G	2B	161.9
4553468|F|0-34:T>G-34:T>G	2B	161.9
3043997|F|0-36:C>G-36:C>G	2B	161.9
3047911|F|0-22:T>C-22:T>C	2B	161.9
3045342|F|0-19:G>A-19:G>A	2B	161.9
11911498|F|0-30:A>G-30:A>G	2B	161.9
3048158|F|0-25:G>A-25:G>A	2B	161.9
3040773|F|0-38:C>T-38:C>T	2B	161.9
4210797|F|0-18:T>G-18:T>G	2B	161.9
3046403|F|0-25:A>G-25:A>G	2B	161.9
3040771|F|0-59:T>C-59:T>C	2B	161.9
4206062|F|0-43:T>C-43:T>C	3B	0
10525156|F|0-33:T>C-33:T>C	3B	0
3623829|F|0-26:T>C-26:T>C	3B	0
3047385|F|0-59:T>G-59:T>G	3B	1.2
4548822|F|0-7:C>T-7:C>T	3B	2.4
3042220|F|0-29:C>T-29:C>T	3B	3.2
3623465|F|0-28:A>C-28:A>C	3B	7.1

3623547|F|0-37:C>G-37:C>G	3B	7.1
8539430|F|0-44:T>G-44:T>G	3B	8.5
4566550|F|0-39:T>G-39:T>G	3B	9.9
3045739|F|0-26:C>G-26:C>G	3B	10.9
14474486|F|0-20:G>C-20:G>C	3B	12.6
3613350|F|0-32:T>C-32:T>C	3B	12.6
8539706|F|0-34:C>G-34:C>G	3B	14.7
10525390|F|0-10:A>G-10:A>G	3B	15.5
SSR_GWM533	3B	15.6
8538315|F|0-5:G>T-5:G>T	3B	17.8
4554401|F|0-12:C>T-12:C>T	3B	17.8
3612135|F|0-42:T>G-42:T>G	3B	31.2
4208877|F|0-37:C>T-37:C>T	3B	37.9
3046991|F|0-20:A>G-20:A>G	3B	44
3616847|F|0-47:G>T-47:G>T	3B	49.3
3609296|F|0-24:C>T-24:C>T	3B	49.8
4555442|F|0-20:G>A-20:G>A	3B	51.9
10524972|F|0-56:G>C-56:G>C	3B	53.3
10524243|F|0-32:G>A-32:G>A	3B	59.7
3612466|F|0-31:A>G-31:A>G	3B	67.4
14479870|F|0-26:A>T-26:A>T	3B	67.4
3040737|F|0-45:T>G-45:T>G	3B	72.8
3603806|F|0-24:G>A-24:G>A	3B	75.1
4548433|F|0-9:A>G-9:A>G	3B	76.2
4367239|F|0-38:A>G-38:A>G	3B	77.8
8536359|F|0-13:T>C-13:T>C	3B	78.4
14479678|F|0-40:G>C-40:G>C	3B	78.4
10522275|F|0-14:A>G-14:A>G	3B	78.4
4342828|F|0-7:C>G-7:C>G	3B	78.4
4565144|F|0-28:T>G-28:T>G	3B	81.6
3040755|F|0-59:C>T-59:C>T	3B	90.9
3046599|F|0-25:C>T-25:C>T	3B	91.7
3614684|F|0-53:G>T-53:G>T	3B	94.5
4344494|F|0-12:T>C-12:T>C	3B	94.5
4349831|F|0-26:C>T-26:C>T	3B	96.4
10507360|F|0-64:G>A-64:G>A	3B	97.1
4355510|F|0-14:G>A-14:G>A	3B	100.1
3043632|F|0-23:A>C-23:A>C	3B	102.5
3046830|F|0-16:C>G-16:C>G	3B	102.7
3046376|F|0-5:T>C-5:T>C	3B	105
3618189|F|0-15:G>A-15:G>A	3B	105.3
4203829|F|0-14:G>C-14:G>C	3B	105.3
3046789|F|0-36:A>G-36:A>G	3B	105.3
3613038|F|0-26:T>C-26:T>C	3B	105.3
3040756|F|0-53:A>C-53:A>C	3B	105.3
SSR_GWM493	3B	105.3
3048012|F|0-48:C>A-48:C>A	3B	105.3
14476350|F|0-26:C>G-26:C>G	3B	105.3

10525346|F|0-14:A>T-14:A>T	3B	105.3
4221332|F|0-23:C>T-23:C>T	3B	105.3
8539436|F|0-7:C>T-7:C>T	3B	105.3
4346573|F|0-7:T>C-7:T>C	3B	106.1
8512741|F|0-6:G>A-6:G>A	3B	107.4
8510168|F|0-8:A>G-8:A>G	3B	108.7
4370235|F|0-35:A>G-35:A>G	3B	110.6
4340546|F|0-5:T>C-5:T>C	3B	111.3
3624438|F|0-32:A>C-32:A>C	3B	111.9
4567314|F|0-58:G>C-58:G>C	3B	117.4
4556333|F|0-13:G>A-13:G>A	3B	129.7
3047112|F|0-43:C>G-43:C>G	3B	145.4
4200924|F|0-20:A>G-20:A>G	3B	146
3608532|F|0-14:T>G-14:T>G	3B	147.5
4353853|F|0-14:A>G-14:A>G	3B	147.8
3046248|F|0-11:C>G-11:C>G	3B	149.1
4368313|F|0-58:T>G-58:T>G	5A	10.3
3044451|F|0-13:A>G-13:A>G	5A	15.9
3044668|F|0-23:G>T-23:G>T	5A	35.4
3044323|F|0-30:T>C-30:T>C	5A	60.4
3043615|F|0-6:C>G-6:C>G	5A	64.9
3622389|F|0-26:T>G-26:T>G	5A	66.2
3044443|F|0-41:C>G-41:C>G	5A	67.3
3612827|F|0-13:T>C-13:T>C	5A	67.9
3622789|F|0-8:G>A-8:G>A	5A	71.9
SSR_B56	5A	72.6
4202279|F|0-25:C>T-25:C>T	5A	72.7
3044232|F|0-20:G>T-20:G>T	5A	75.6
3617012|F|0-24:G>C-24:G>C	5A	77.2
8511982|F|0-33:T>C-33:T>C	5A	77.8
4340705|F|0-24:A>T-24:A>T	5A	80
3044642|F|0-5:C>A-5:C>A	5A	80.6
8512585|F|0-47:C>T-47:C>T	5A	80.6
3048217|F|0-26:T>C-26:T>C	5A	80.6
4345993|F|0-50:C>T-50:C>T	5A	80.8
3047343|F|0-35:A>G-35:A>G	5A	81.3
4341775|F|0-14:G>A-14:G>A	5A	81.4
8511754|F|0-18:A>G-18:A>G	5A	81.4
8511754|F|0-8:T>C-8:T>C	5A	81.4
4209786|F|0-20:T>A-20:T>A	5A	81.4
4209303|F|0-13:C>G-13:C>G	5A	81.4
SSR_B180	5A	82.4
4358304|F|0-13:T>G-13:T>G	5A	82.4
4208849|F|0-14:T>G-14:T>G	5A	82.6
3043582|F|0-8:T>C-8:T>C	5A	85
19758850|F|0-25:T>C-25:T>C	5A	85
4369263|F|0-48:G>C-48:G>C	5A	85
4556655|F|0-8:C>T-8:C>T	5A	85

4211970|F|0-17:G>C-17:G>C	5A	106.3
10510387|F|0-11:G>A-11:G>A	5A	106.3
8510980|F|0-43:C>T-43:C>T	5A	108.8
10524750|F|0-19:C>G-19:C>G	5A	114.6
3043111|F|0-18:A>G-18:A>G	5A	122.6
4369809|F|0-25:C>T-25:C>T	5A	123.2
8510566|F|0-24:T>C-24:T>C	5A	123.8
3048231|F|0-59:A>G-59:A>G	5A	124.9
14476192|F|0-16:G>A-16:G>A	5A	127.1
4564410|F|0-5:T>C-5:T>C	5A	127.8
4369428|F|0-18:T>C-18:T>C	5A	130.8
3618419|F|0-12:C>T-12:C>T	5A	131.4
3042912|F|0-22:C>T-22:C>T	5A	131.8
10519396|F|0-10:A>G-10:A>G	5A	139
3043439|F|0-42:A>C-42:A>C	5A	141.9
3043887|F|0-43:T>C-43:T>C	5A	143.7
3041628|F|0-34:A>G-34:A>G	5A	145.3
8536847|F|0-31:C>G-31:C>G	5A	150.4
4349070|F|0-19:A>G-19:A>G	5A	150.4
3047420|F|0-46:T>C-46:T>C	5A	152.9
3042383|F|0-68:C>A-68:C>A	5A	154.1
4368543|F|0-12:T>C-12:T>C	5A	155.3
3041551|F|0-68:G>T-68:G>T	5A	156.4
11910690|F|0-10:A>G-10:A>G	5A	158.1
8512997|F|0-15:G>C-15:G>C	5A	161.7
3045186|F|0-23:C>G-23:C>G	5A	161.9
3619312|F|0-12:G>C-12:G>C	5A	164.2
4339983|F|0-40:G>T-40:G>T	5A	167.7
4358724|F|0-28:C>A-28:C>A	5A	167.7
3616918|F|0-7:C>G-7:C>G	5A	167.7
4368950|F|0-35:C>G-35:C>G	5A	167.7
4206836|F|0-29:C>G-29:C>G	5A	168.6
3041413|F|0-24:C>T-24:C>T	5A	169.2
3616438|F|0-45:C>T-45:C>T	5A	171.5
3621575|F|0-12:A>G-12:A>G	5A	171.6
3040691|F|0-52:C>A-52:C>A	5A	171.6
8511829|F|0-24:G>C-24:G>C	5R	30.4
10507075|F|0-66:G>C-66:G>C	5R	32.2
8510162|F|0-40:C>T-40:C>T	5R	32.5
4203295|F|0-11:T>A-11:T>A	5R	33.7
15998544|F|0-21:G>C-21:G>C	5R	34.6
4370061|F|0-47:C>G-47:C>G	5R	36.4
4358777|F|0-13:T>G-13:T>G	5R	37.2
3047741|F|0-43:C>A-43:C>A	5R	38.4
4210475|F|0-54:T>C-54:T>C	5R	41.6
3041225|F|0-17:T>A-17:T>A	5R	42.2
3040767|F|0-6:C>T-6:C>T	5R	43.6
8510762|F|0-17:C>T-17:C>T	5R	45

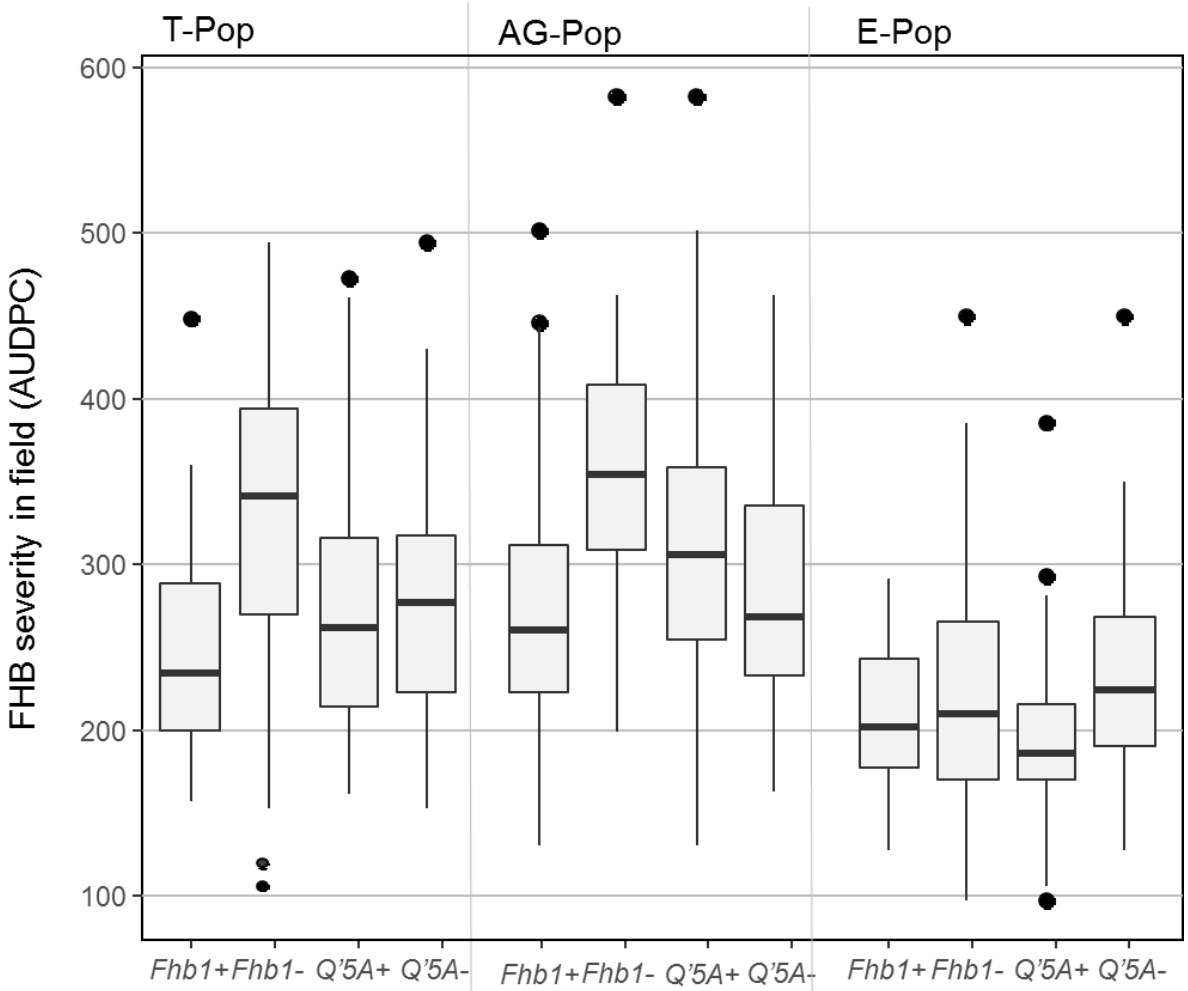
4215785|F|0-9:T>G-9:T>G	5R	46.7
4368460|F|0-9:G>T-9:G>T	5R	47.6
3619923|F|0-47:G>A-47:G>A	5R	49
4215609|F|0-37:G>A-37:G>A	5R	49.1
3044240|F|0-45:C>G-45:C>G	5R	51
8533380|F|0-13:C>G-13:C>G	5R	52.3
3046128|F|0-28:C>G-28:C>G	5R	54.4
8511622|F|0-5:C>A-5:C>A	5R	54.9
4213814|F|0-24:A>T-24:A>T	5R	55
3618115|F|0-24:G>C-24:G>C	5R	56.9
8535839|F|0-9:C>G-9:C>G	5R	57.8
3615271|F|0-15:G>C-15:G>C	5R	59.7
4572801|F|0-26:G>A-26:G>A	5R	61.4
4339290|F|0-10:G>C-10:G>C	5R	61.8
4200926|F|0-6:T>C-6:T>C	5R	64
10520222|F|0-9:C>T-9:C>T	5R	64.1
3604134|F|0-27:G>A-27:G>A	5R	64.9
4218413|F|0-29:G>T-29:G>T	5R	65
8537234|F|0-28:A>C-28:A>C	5R	66.8
4355950|F|0-17:A>C-17:A>C	5R	68.9
4358372|F|0-13:T>G-13:T>G	5R	74.7
4551383|F|0-32:G>C-32:G>C	5R	74.7
10509424|F|0-13:A>T-13:A>T	5R	74.7
4212683|F|0-12:G>C-12:G>C	5R	74.7
4354271|F|0-37:G>C-37:G>C	5R	74.7
3043065|F|0-17:C>T-17:C>T	5R	75.4
Xiac0130	5R	78.2
4368305|F|0-34:G>C-34:G>C	5R	79.4
16312805|F|0-9:A>C-9:A>C	5R	79.4
4217803|F|0-32:A>G-32:A>G	5R	79.4
8537991|F|0-19:T>C-19:T>C	5R	79.4
Xiac0132	5R	79.4
Xiac_131	5R	79.4
Xiac0129	5R	79.4
Xiac0134	5R	79.4
Xiac0135	5R	79.4
3614221|F|0-5:A>G-5:A>G	5R	79.4
4550653|F|0-16:G>C-16:G>C	5R	83.3
3048220|F|0-5:T>C-5:T>C	5R	86.7
3622112|F|0-32:A>C-32:A>C	5R	89.1
8510861|F|0-8:C>G-8:C>G	5R	89.8
3613461|F|0-15:T>C-15:T>C	5R	90.3
4218144|F|0-24:T>C-24:T>C	5R	91.9
3041126|F|0-31:A>G-31:A>G	5R	93.5
3616689|F|0-13:G>C-13:G>C	5R	94
4342949|F|0-42:G>A-42:G>A	5R	96
3041777|F|0-14:C>A-14:C>A	5R	97.2
4214907|F|0-31:A>C-31:A>C	5R	98.6

4372334|F|0-23:C>T-23:C>T	5R	101.6
3045841|F|0-29:A>G-29:A>G	5R	101.7
8510155|F|0-5:T>G-5:T>G	5R	101.7
8511234|F|0-17:T>G-17:T>G	5R	101.7
8537768|F|0-18:T>C-18:T>C	5R	104.2
3044240|F|0-32:T>A-32:T>A	5R	104.6
8535029|F|0-17:T>A-17:T>A	5R	104.6
4364448|F|0-9:G>C-9:G>C	5R	107.1
4548418|F|0-7:G>A-7:G>A	5R	107.1
10511507|F|0-5:T>A-5:T>A	5R	112.6
3613671|F|0-61:T>C-61:T>C	5R	112.6
8511883|F|0-37:C>T-37:C>T	5R	112.6
3613715|F|0-10:T>A-10:T>A	5R	112.6
10508623|F|0-54:G>A-54:G>A	5R	112.6
4367516|F|0-13:C>G-13:C>G	5R	112.6
3041059|F|0-29:C>A-29:C>A	5R	113.6
3617226|F|0-11:T>C-11:T>C	5R	117.4
16356147|F|0-12:A>T-12:A>T	5R	119.3
8509926|F|0-53:G>C-53:G>C	5R	121
4368984|F|0-41:G>A-41:G>A	5R	121.1
10511847|F|0-30:G>C-30:G>C	5R	123.1
4349077|F|0-16:A>G-16:A>G	5R	125.5
3047859|F|0-32:A>T-32:A>T	5R	126.8
4372582|F|0-6:C>G-6:C>G	5R	130.2
3624076|F|0-23:G>A-23:G>A	5R	135.6
10522522|F|0-14:C>G-14:C>G	5R	139.1
4342343|F|0-17:A>G-17:A>G	5R	143.5
4369388|F|0-16:C>G-16:C>G	5R	147.1
3623312|F|0-68:T>C-68:T>C	5R	148.4
4215269|F|0-13:C>G-13:C>G	5R	151.7
4372663|F|0-19:C>T-19:C>T	5R	157.1
3606139|F|0-6:T>C-6:T>C	5R	161.1
3616658|F|0-7:T>C-7:T>C	5R	165.3
4343052|F|0-32:T>C-32:T>C	5R	165.3
4349596|F|0-19:A>G-19:A>G	5R	169
4203815|F|0-10:A>G-10:A>G	5R	171.9
10521923|F|0-28:C>G-28:C>G	5R	174.9
10524133|F|0-33:C>T-33:C>T	5R	178.4
14479933|F|0-8:C>A-8:C>A	5R	180.1
10521057|F|0-10:A>C-10:A>C	5R	182.5
16358671|F|0-14:A>C-14:A>C	5R	189.8
4212656|F|0-33:G>A-33:G>A	5R	194.9
3608227|F|0-48:G>A-48:G>A	5R	194.9
10508847|F|0-59:T>C-59:T>C	5R	196
4564732|F|0-22:C>G-22:C>G	7A	0
3047410|F|0-56:G>A-56:G>A	7A	0
3047348|F|0-9:C>T-9:C>T	7A	0
4350450|F|0-11:T>C-11:T>C	7A	0

3045662|F|0-37:A>C-37:A>C	7A	0
8510339|F|0-25:A>C-25:A>C	7A	0
4345289|F|0-18:A>T-18:A>T	7A	0
4365444|F|0-17:C>G-17:C>G	7A	0
8538497|F|0-5:G>A-5:G>A	7A	0
4365701|F|0-33:G>A-33:G>A	7A	0
3043390|F|0-46:C>T-46:C>T	7A	0
3041321|F|0-63:A>G-63:A>G	7A	0
3044826|F|0-60:A>G-60:A>G	7A	0
3040781|F|0-29:C>T-29:C>T	7A	0
3620501|F|0-51:T>C-51:T>C	7A	0
3047209|F|0-25:C>T-25:C>T	7A	0
3045621|F|0-68:A>G-68:A>G	7A	0
8510968|F|0-15:C>T-15:C>T	7A	0
4575453|F|0-46:T>C-46:T>C	7A	0
3617251|F|0-10:G>C-10:G>C	7A	0.2
3048180|F|0-6:T>C-6:T>C	7A	1.6
3046073|F|0-6:T>C-6:T>C	7A	1.6
4365299|F|0-18:G>A-18:G>A	7A	1.8
4546240|F|0-7:A>G-7:A>G	7A	2.1
4208214|F|0-52:C>T-52:C>T	7A	2.1
3046262|F|0-53:G>C-53:G>C	7A	2.1
4216793|F|0-25:G>A-25:G>A	7A	2.2
4366897|F|0-21:A>C-21:A>C	7A	2.2
8510360|F|0-7:G>A-7:G>A	7A	2.2
3619224|F|0-27:G>A-27:G>A	7A	2.2
3613527|F|0-27:T>C-27:T>C	7A	3.2
3621171|F|0-11:T>A-11:T>A	7A	3.4
3606651|F|0-14:G>A-14:G>A	7A	3.4
3040817|F|0-66:T>G-66:T>G	7A	4
19759127|F|0-20:T>G-20:T>G	7A	4
8535359|F|0-35:C>G-35:C>G	7A	4
3610348|F|0-12:G>C-12:G>C	7A	4
4368103|F|0-61:G>A-61:G>A	7A	4
3040859|F|0-10:A>G-10:A>G	7A	4
4207133|F|0-7:G>A-7:G>A	7A	4
4346295|F|0-22:A>G-22:A>G	7A	4
3043802|F|0-48:G>A-48:G>A	7A	4
10524688|F|0-21:A>G-21:A>G	7A	4
4549474|F|0-30:A>G-30:A>G	7A	4
4212270|F|0-11:T>C-11:T>C	7A	4
3044254|F|0-49:T>C-49:T>C	7A	4
3042384|F|0-16:C>A-16:C>A	7A	4
4218019|F|0-65:T>A-65:T>A	7A	4
3044607|F|0-8:T>C-8:T>C	7A	4.7
4210132|F|0-27:C>G-27:C>G	7A	4.7
4212761|F|0-44:A>G-44:A>G	7A	5
3046683|F|0-21:T>C-21:T>C	7A	7.3

3046716|F|0-33:C>T-33:C>T	7A	8.5
3045484|F|0-39:G>C-39:G>C	7A	11.5
3041327|F|0-55:T>C-55:T>C	7A	12.4
4354035|F|0-14:A>G-14:A>G	7A	30.2
3042820|F|0-35:A>C-35:A>C	7A	37.2
4212233|F|0-6:G>A-6:G>A	7A	40.9
3041789|F|0-49:C>G-49:C>G	7A	49.5
8512212|F|0-5:T>C-5:T>C	7A	119
4358654|F|0-16:A>G-16:A>G	7A	121.7
4566440|F|0-15:G>A-15:G>A	7A	125.5
4210707|F|0-55:C>T-55:C>T	7A	126
19759597|F|0-9:C>T-9:C>T	7A	233.2
4214399|F|0-28:T>C-28:T>C	7A	342.5
8509727|F|0-17:C>A-17:C>A	7A	342.5
10521319|F|0-6:A>G-6:A>G	7A	344.4
3043440|F|0-22:G>A-22:G>A	7A	344.9
11912988|F|0-7:G>A-7:G>A	7A	345.6
3048200|F|0-53:G>C-53:G>C	7A	347
8509724|F|0-44:T>C-44:T>C	7A	347.6
19759008|F|0-60:T>C-60:T>C	7A	347.7
8511596|F|0-5:G>A-5:G>A	7A	347.9
4565419|F|0-47:G>T-47:G>T	7A	348.5
3046877|F|0-43:T>C-43:T>C	7A	349.5

ESM_6 : Box plot distributions of F_4 according to their alleles at *Fhb1* and *Qfhs.ifa-5A* loci for the three tested populations based on BLUEs of FHB severity in field (AUDPC). BLUEs were calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations FHB severity in field (AUDPC) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.



Number of lines73	39	23	39	39	42	30	46	42	23	54	42	34
AUDPC mean	251[a]	335[b]	277[ab]	280[ab]	279[a]	356[b]	312[ab]	285[ab]	208[a]	222[a]	198[a]	235[a]
AUDPC sd	63	88	81	77	77	82	88	69	43	73	57	65

ESM_7 : Additional information regarding the FHB resistance QTL detected on chromosome 2B, with **(A)** the blasting information of the markers present in the confidence interval of the QTL, and **(B)** the functional annotation of the 48 high confidence genes present in the confidence interval of the QTL

Part A: Blasting information of the markers present in the confidence interval of the FHB resistance QTL detected on chromosome 2B

		Blast on the wheat physical map				Position (cM) on the 2B	Position (cM) on the 2B
CloneID	TrimmedSequence	start	end	Score	%ID		
3042042|F|0-5:T>A-5:T>A	TGCAGTGCAGCGTTACCCAACCCAAACCATGTCCTTGCTCAACAAAGCCAAACGTTTTGATCGAAACTC	12627	12559	125	100	60.60	149.1
3046194|F|0-31:A>G-31:A>G	TGCAGGGTCGGGCGTATGCGTACCACTGGATATGTGCGTGTGGGCACTGTGGCGTTCAGCGCCAGCCAG	8697	8629	125	100	59.70	147.8
3041167|F|0-65:G>T-65:G>T	TGCAGTACTATACTACGCAGTAACGCAAGCGCAAGATCTGTCAGCAAGTGCGACTTCCTAGTGCAGATC	7894	7826	120	99	59.70	147.1
3041025|F|0-45:C>G-45:C>G	TGCAGGAAGATAATGCTCAAGGTGAGATCTTCAGACAACCATCATCTGTAAGCTGTGCATTGTACCCGA	7251	7184	118	99	55.60	-
4372487|F|0-26:T>G-26:T>G	TGCAGCCCGCGAACCGCGCGATGCGCTCCATGTACGCGCGCACCGAGATGTCGGGCTTCGTCATCGCCC	4153	4085	125	100	57.60	142.7
3048234|F|0-31:T>C-31:T>C	TGCAGGCCACCCCCTTCGCCGTGTGCACCACTATCACCACCCCCGCCGAACGCCGCACCCGCACGCCAT	2961	2893	125	100	58.50	144.8
10517361|F|0-33:T>C-33:T>C	**TGCAGACACCTGCGACGGCGAGGAGGCCTGCGGTGGTGATTTGACCGTGGTCGGCGCCGCGGCGAATGT**	**2204**	**2272**	**120**	**99**	**58.30**	**144.00**
4208573|F|0-11:C>T-11:C>T	TGCAGTACATGCAGTTTTGGTGCAGAGAAAGCGGCGGCGACGAGGACCCG	1859	1810	91.5	100	53.80	-
11911490|F|0-41:G>T-41:G>T	**TGCAGGAGTCGGCGTTGCAGGGGCTGGTGCTGTTCCCTTCTGCCTCCTCCTGACCCGACGGCGCGGGGG**	**1495**	**1563**	**125**	**100**	**60.60**	**149.7**
4568188|F|0-23:G>A-23:G>A	TGCAGTGGTTCGGGGACAGCAGCGGCCAGGCCGCGCCG	1314	1277	69.8	100	64.40	160.8
11911705|F|0-32:A>G-32:A>G	TGCAGCAGCTTGTCGGGGCGGCGGGAGGAGGCACTCGGGAGCCGAAGACGGCGGCCG	1245	1301	104	100	61.00	150.4

Markers in bolt have been identified as the closest of the QTL (cf Table 5&6)

Part B: Functional annotation of the 48 high confidence genes present in the confidence interval of the FHB resistance QTL detected on chromosome 2B

Interval limits: 582810429 to 591967253 on chr 2B of the bread wheat physical map

- TraesCS2B01G409500.1 1 --* AT5G41220.3 glutathione S-transferase THETA 3 G
- TraesCS2B01G409600.1 1 *-* sp|O60016|CLR4_SCHPO Histone-lysine N-methyltransferase, H3 lysine-9 specific PF02182: SAD/SRA domain; PF05033: Pre-SET motif; PF00856: SET domain IPR001214: SET domain; IPR003105: SRA-YDG; IPR003616: Post-SET domain; IPR007728: Pre-SET domain; IPR015947: PUA-like domain GO:0005515 MF: protein binding;GO:0005634 CC: nucleus;GO:0008270 MF: zinc ion binding;GO:0018024 MF: histone-lysine N-methyltransferase activity;GO:0034968 BP: histone lysine methylation;GO:0042393 MF: histone binding G PF02182; PF05033; PF00856 IPR001214; IPR003105; IPR003616; IPR007728; IPR015947 GO:0005515; GO:0005634; GO:0008270; GO:0018024; GO:0034968; GO:0042393
- TraesCS2B01G409700.1 1 *-* tr|D7LDA2|D7LDA2_ARALL Kinase family protein PF12436: ICP0-binding domain of Ubiquitin-specific protease 7; PF07714: Protein tyrosine kinase; PF04564: U-box domain IPR000719: Protein kinase domain; IPR001245: Serine-threonine/tyrosine-protein kinase, catalytic domain; IPR003613: U box domain; IPR008266: Tyrosine-protein kinase, active site; IPR011009: Protein kinase-like domain; IPR013083: Zinc finger, RING/FYVE/PHD-type; IPR024729: Ubiquitin carboxyl-terminal hydrolase 7, ICP0-binding domain GO:0004672 MF: protein kinase activity;GO:0004842 MF: ubiquitin-protein transferase activity;GO:0005524 MF: ATP binding;GO:0006468 BP: protein

phosphorylation;GO:0016567 BP: protein ubiquitination G PF12436; PF07714; PF04564 IPR000719; IPR001245; IPR003613; IPR008266; IPR011009; IPR013083; IPR024729 GO:0004672; GO:0004842; GO:0005524; GO:0006468; GO:0016567

- TraesCS2B01G409800.1 1 *** tr|A0A061E0T1|A0A061E0T1_THECC Alpha/beta-Hydrolases superfamily protein, putative PF07859: alpha/beta hydrolase fold IPR013094: Alpha/beta hydrolase fold-3; IPR029058: Alpha/Beta hydrolase fold GO:0008152 BP: metabolic process;GO:0016787 MF: hydrolase activity G PF07859 IPR013094; IPR029058 GO:0008152; GO:0016787
- TraesCS2B01G409900.1 1 *** tr|A0A1D1Y0Z2|A0A1D1Y0Z2_9ARAE HAUS augmin-like complex subunit 6 PF14661: HAUS augmin-like complex subunit 6 N-terminus IPR028163: HAUS augmin-like complex subunit 6, N-terminal G PF14661 IPR028163
- TraesCS2B01G410000.1 1 *** tr|Q6H3X9|Q6H3X9_ORYSJ Cyclin-like PF08613: Cyclin IPR013763: Cyclin-like; IPR013922: Cyclin PHO80-like GO:0000079 BP: regulation of cyclin-dependent protein serine/threonine kinase activity;GO:0019901 MF: protein kinase binding G PF08613 IPR013763; IPR013922 GO:0000079; GO:0019901
- TraesCS2B01G410100.1 1 *** tr|A0A1E5V1R5|A0A1E5V1R5_9POAL Pentatricopeptide repeat-containing protein PF13812: Pentatricopeptide repeat domain; PF13181: Tetratricopeptide repeat; PF01535: PPR repeat IPR002885: Pentatricopeptide repeat; IPR011990: Tetratricopeptide-like helical domain; IPR019734: Tetratricopeptide repeat GO:0005515 MF: protein binding G PF13812; PF13181; PF01535 IPR002885; IPR011990; IPR019734 GO:0005515
- TraesCS2B01G410200.1 0 *-* tr|B9SYZ6|B9SYZ6_RICCO GATA transcription factor, putative PF00320: GATA zinc finger IPR000679: Zinc finger, GATA-type; IPR013088: Zinc finger, NHR/GATA-type GO:0003700 MF: transcription factor activity, sequence-specific DNA binding;GO:0006355 BP: regulation of transcription, DNA-templated;GO:0008270 MF: zinc ion binding;GO:0043565 MF: sequence-specific DNA binding G PF00320 IPR000679; IPR013088 GO:0003700; GO:0006355; GO:0008270; GO:0043565
- TraesCS2B01G410300.1 1 *** tr|W5BBW5|W5BBW5_WHEAT Mannosyltransferase PF03901: Alg9-like mannosyltransferase family IPR005599: GPI mannosyltransferase GO:0016757 MF: transferase activity, transferring glycosyl groups G PF03901 IPR005599 GO:0016757
- TraesCS2B01G410400.1 1 *** tr|A0A060D828|A0A060D828_MAIZE WRKY transcription factor PF03106: WRKY DNA -binding domain IPR003657: WRKY domain GO:0003700 MF: transcription factor activity, sequence-specific DNA binding;GO:0006355 BP: regulation of transcription, DNA-templated;GO:0043565 MF: sequence-specific DNA binding G PF03106 IPR003657 GO:0003700; GO:0006355; GO:0043565
- TraesCS2B01G410500.1 1 *-* AT4G04025.1 transcription repressor PF13724: DNA-binding domain; PF04844: Transcriptional repressor, ovate IPR006458: Ovate protein family, C-terminal; IPR025830: DNA-binding domain, ovate family-like GO:0003677 MF: DNA binding G PF13724; PF04844 IPR006458; IPR025830 GO:0003677
- TraesCS2B01G410600.1 1 *-* tr|B9SKK4|B9SKK4_RICCO ELMO domain-containing protein, putative PF04727: ELMO/CED-12 family IPR006816: ELMO domain; IPR012674: Calycin G PF04727 IPR006816; IPR012674
- TraesCS2B01G410700.1 1 --* tr|A0A061RJC0|A0A061RJC0_9CHLO Ubiquitous surface protein a2h G
- TraesCS2B01G410800.1 1 *** tr|M7YXH9|M7YXH9_TRIUA Blue copper protein PF02298: Plastocyanin-like domain IPR003245: Phytocyanin

domain; IPR008972: Cupredoxin GO:0009055 MF: electron carrier activity G PF02298 IPR003245; IPR008972 GO:0009055

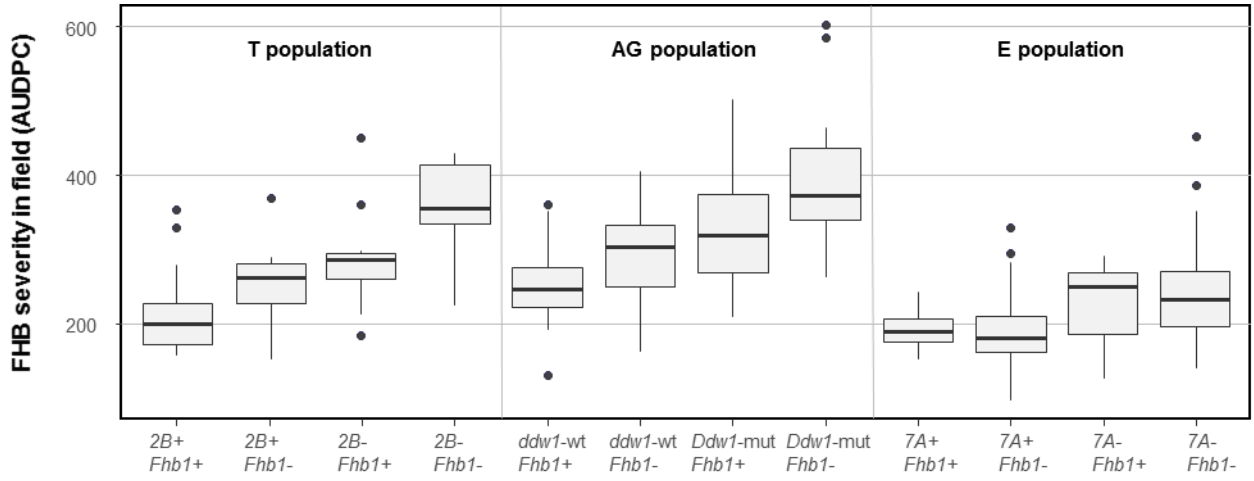
- TraesCS2B01G410900.1 1 *** tr|A0A199VV55|A0A199VV55_ANACO Protein ROOT PRIMORDIUM DEFECTIVE 1 PF11955: Plant organelle RNA recognition domain IPR021099: Plant organelle RNA recognition domain G PF11955 IPR021099
- TraesCS2B01G411000.1 1 *** tr|B9GP63|B9GP63_POPTR Kinase family protein PF00069: Protein kinase domain IPR000719: Protein kinase domain; IPR008271: Serine/threonine-protein kinase, active site; IPR011009: Protein kinase-like domain GO:0004672 MF: protein kinase activity;GO:0005524 MF: ATP binding;GO:0006468 BP: protein phosphorylation G PF00069 IPR000719; IPR008271; IPR011009 GO:0004672; GO:0005524; GO:0006468
- TraesCS2B01G411100.1 1 *** tr|W5B7G6|W5B7G6_WHEAT Ubiquitin carboxyl-terminal hydrolase PF01088: Ubiquitin carboxyl-terminal hydrolase, family 1 IPR001578: Peptidase C12, ubiquitin carboxyl-terminal hydrolase GO:0004843 MF: thiol-dependent ubiquitin-specific protease activity;GO:0005622 CC: intracellular;GO:0006511 BP: ubiquitin-dependent protein catabolic process G PF01088 IPR001578 GO:0004843; GO:0005622; GO:0006511
- **TraesCS2B01G411200.1 1 *-* tr|A0A072VQ89|A0A072VQ89_MEDTR Cysteine-rich receptor-kinase-like protein PF01657: Salt stress response/antifungal IPR002902: Gnk2-homologous domain G PF01657 IPR002902**
- **TraesCS2B01G411300.1 1 *-* tr|A0A072VQ98|A0A072VQ98_MEDTR Cysteine-rich receptor-kinase-like protein PF01657: Salt stress response/antifungal IPR002902: Gnk2-homologous domain G PF01657 IPR002902**
- **TraesCS2B01G411400.1 1 *-* tr|A0A072VRC1|A0A072VRC1_MEDTR Cysteine-rich receptor-kinase-like protein PF01657: Salt stress response/antifungal IPR002902: Gnk2-homologous domain G PF01657 IPR002902**
- TraesCS2B01G411500.1 1 *** tr|F2Y9E9|F2Y9E9_COFAR Ethylene-responsive transcription factor PF00847: AP2 domain IPR001471: AP2/ERF domain; IPR016177: DNA-binding domain GO:0003677 MF: DNA binding;GO:0003700 MF: transcription factor activity, sequence-specific DNA binding;GO:0006355 BP: regulation of transcription, DNA-templated G PF00847 IPR001471; IPR016177 GO:0003677; GO:0003700; GO:0006355
- TraesCS2B01G411600.1 1 *** tr|K7VQC2|K7VQC2_MAIZE Histone H4 PF15511: Centromere kinetochore component CENP-T histone fold IPR001951: Histone H4; IPR009072: Histone-fold; IPR019809: Histone H4, conserved site GO:0000786 CC: nucleosome;GO:0003677 MF: DNA binding;GO:0005634 CC: nucleus;GO:0006334 BP: nucleosome assembly;GO:0046982 MF: protein heterodimerization activity G PF15511 IPR001951; IPR009072; IPR019809 GO:0000786; GO:0003677; GO:0005634; GO:0006334; GO:0046982
- TraesCS2B01G411700.1 1 *** tr|Q9ZP33|Q9ZP33_SOLLC Expansin PF03330: Lytic transglycolase; PF01357: Pollen allergen IPR002963: Expansin; IPR007112: Expansin/pollen allergen, DPBB domain; IPR007117: Expansin, cellulose-binding-like domain; IPR007118: Expansin/Lol pI; IPR009009: RlpA-like protein, double-psi beta-barrel domain GO:0005576 CC: extracellular region;GO:0009664 BP: plant-type cell wall organization G PF03330; PF01357 IPR002963; IPR007112; IPR007117; IPR007118; IPR009009 GO:0005576; GO:0009664
- TraesCS2B01G411800.1 1 *-* tr|A0A061GIQ6|A0A061GIQ6_THECC Oxidative stress 3, putative isoform 2 G

- TraesCS2B01G411900.1 1 *** tr|A0A1E5V6C5|A0A1E5V6C5_9POAL Pentatricopeptide repeat-containing protein PF01535: PPR repeat; PF12854: PPR repeat; PF13041: PPR repeat family IPR002885: Pentatricopeptide repeat; IPR011990: Tetratricopeptide-like helical domain GO:0005515 MF: protein binding G PF01535; PF12854; PF13041 IPR002885; IPR011990 GO:0005515
- TraesCS2B01G412000.1 1 *** tr|F4K5W5|F4K5W5_ARATH p-loop containing nucleoside triphosphate hydrolases superfamily protein PF13086: AAA domain; PF13087: AAA domain IPR027417: P-loop containing nucleoside triphosphate hydrolase G PF13086; PF13087 IPR027417
- TraesCS2B01G412100.1 0 *** tr|F4IBK8|F4IBK8_ARATH p-loop containing nucleoside triphosphate hydrolases superfamily protein PF13086: AAA domain; PF13087: AAA domain IPR027417: P-loop containing nucleoside triphosphate hydrolase G PF13086; PF13087 IPR027417
- TraesCS2B01G412200.1 1 *** tr|F4K5W5|F4K5W5_ARATH p-loop containing nucleoside triphosphate hydrolases superfamily protein PF13086: AAA domain; PF13087: AAA domain IPR027417: P-loop containing nucleoside triphosphate hydrolase G PF13086; PF13087 IPR027417
- TraesCS2B01G412300.1 1 *-* tr|A0A1E5UVG9|A0A1E5UVG9_9POAL Armadillo repeat-containing protein 8 G
- **TraesCS2B01G412400.1 1 *** tr|A0A1D1XUJ9|A0A1D1XUJ9_9ARAE Antimicrobial peptide 1 PF09117: MiAMP1 IPR011024: Gamma-crystallin-related; IPR015201: Antimicrobial protein MiAMP1; IPR015791: Antimicrobial/protein inhibitor, gamma-crystallin-like GO:0006952 BP: defense response;GO:0045926 BP: negative regulation of growth G PF09117 IPR011024; IPR015201; IPR015791 GO:0006952; GO:0045926**
- TraesCS2B01G412500.1 1 *-* AT4G27590.2 Heavy metal transport/detoxification superfamily protein PF00403: Heavy-metal-associated domain IPR006121: Heavy metal-associated domain, HMA GO:0030001 BP: metal ion transport;GO:0046872 MF: metal ion binding G PF00403 IPR006121 GO:0030001; GO:0046872
- TraesCS2B01G412600.1 1 --* AT4G34310.9 alpha/beta-Hydrolases superfamily protein G
- TraesCS2B01G412700.1 1 *** tr|A0A1E5V6G8|A0A1E5V6G8_9POAL B3 domain-containing protein PF02362: B3 DNA binding domain IPR003340: B3 DNA binding domain; IPR015300: DNA-binding pseudobarrel domain GO:0003677 MF: DNA binding G PF02362 IPR003340; IPR015300 GO:0003677
- TraesCS2B01G412800.1 1 --* sp|A8AP95|IDI_CITK8 Isopentenyl-diphosphate Delta-isomerase G
- TraesCS2B01G412900.1 1 *** tr|A0A061E8F9|A0A061E8F9_THECC 2-oxoglutarate and Fe(II)-dependent oxygenase superfamily protein PF14226: non-haem dioxygenase in morphine synthesis N-terminal; PF03171: 2OG-Fe(II) oxygenase superfamily IPR005123: Oxoglutarate/iron-dependent dioxygenase; IPR026992: Non-haem dioxygenase N-terminal domain; IPR027443: Isopenicillin N synthase-like GO:0016491 MF: oxidoreductase activity;GO:0055114 BP: oxidation-reduction process G PF14226; PF03171 IPR005123; IPR026992; IPR027443 GO:0016491; GO:0055114
- TraesCS2B01G413000.1 1 *** tr|A0A061G1L6|A0A061G1L6_THECC 2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein PF14226: non-haem dioxygenase in morphine synthesis N-terminal; PF03171: 2OG-Fe(II) oxygenase superfamily IPR005123: Oxoglutarate/iron-dependent dioxygenase; IPR026992: Non-haem dioxygenase N-terminal domain; IPR027443: Isopenicillin N synthase-like GO:0016491 MF: oxidoreductase activity;GO:0055114 BP:

oxidation-reduction process G PF14226; PF03171 IPR005123; IPR026992; IPR027443 GO:0016491; GO:0055114

- TraesCS2B01G413100.1 1 *-* tr|A0A061GXP2|A0A061GXP2_THECC RING/U-box superfamily protein, putative PF13639: Ring finger domain IPR001841: Zinc finger, RING-type; IPR011016: Zinc finger, RING-CH-type; IPR013083: Zinc finger, RING/FYVE/PHD-type GO:0005515 MF: protein binding;GO:0008270 MF: zinc ion binding G PF13639 IPR001841; IPR011016; IPR013083 GO:0005515; GO:0008270
- TraesCS2B01G413200.1 1 *-* AT1G63840.1 RING/U-box superfamily protein PF13639: Ring finger domain IPR001841: Zinc finger, RING-type; IPR011016: Zinc finger, RING-CH-type; IPR013083: Zinc finger, RING/FYVE/PHD-type GO:0005515 MF: protein binding;GO:0008270 MF: zinc ion binding G PF13639 IPR001841; IPR011016; IPR013083 GO:0005515; GO:0008270
- TraesCS2B01G413300.1 1 --* tr|N0GUM4|N0GUM4_9CARY DUF1191 superfamily protein PF06697: Protein of unknown function (DUF1191) IPR010605: Protein of unknown function DUF1191 G PF06697 IPR010605
- TraesCS2B01G413400.1 1 *** tr|A8J0P9|A8J0P9_CHLRE E2 ubiquitin-conjugating-like enzyme PF00179: Ubiquitin-conjugating enzyme IPR000608: Ubiquitin-conjugating enzyme E2; IPR016135: Ubiquitin-conjugating enzyme/RWD-like G PF00179 IPR000608; IPR016135
- TraesCS2B01G413500.1 1 *** tr|A0A060CY61|A0A060CY61_MAIZE GRAS transcription factor PF03514: GRAS domain family IPR005202: Transcription factor GRAS G PF03514 IPR005202
- TraesCS2B01G413600.1 1 *** tr|A0A1E5UMR2|A0A1E5UMR2_9POAL BTB/POZ domain-containing protein IPR000210: BTB/POZ domain; IPR011333: SKP1/BTB/POZ domain GO:0005515 MF: protein binding G IPR000210; IPR011333 GO:0005515
- TraesCS2B01G413700.1 1 *** AT4G22060.1 F-box protein (DUF295) PF03478: Protein of unknown function (DUF295) IPR001810: F-box domain; IPR005174: Domain unknown function DUF295 GO:0005515 MF: protein binding TE? PF03478 IPR001810; IPR005174 GO:0005515
- TraesCS2B01G413800.1 1 *-* tr|A0A0K9NM69|A0A0K9NM69_ZOSMR RING finger protein PF13639: Ring finger domain IPR001841: Zinc finger, RING-type; IPR011016: Zinc finger, RING-CH-type; IPR013083: Zinc finger, RING/FYVE/PHD-type GO:0005515 MF: protein binding;GO:0008270 MF: zinc ion binding G PF13639 IPR001841; IPR011016; IPR013083 GO:0005515; GO:0008270
- TraesCS2B01G413900.1 1 *** tr|W9SHU8|W9SHU8_9ROSA Werner Syndrome-like exonuclease PF01612: 3'-5' exonuclease IPR002562: 3'-5' exonuclease domain; IPR012337: Ribonuclease H-like domain GO:0003676 MF: nucleic acid binding;GO:0006139 BP: nucleobase-containing compound metabolic process;GO:0008408 MF: 3'-5' exonuclease activity G PF01612 IPR002562; IPR012337 GO:0003676; GO:0006139; GO:0008408
- TraesCS2B01G414000.1 1 --* sp|A6RVU0|EFG1P_BOTFB rRNA-processing protein efg1 G
- TraesCS2B01G414100.1 1 *** tr|A0A0B0MIB4|A0A0B0MIB4_GOSAR Beta-1,3-N-acetylglucosaminyltransferase lunatic fringe PF04646: Protein of unknown function, DUF604 IPR006740: Protein of unknown function DUF604 G PF04646 IPR006740
- TraesCS2B01G414200.1 1 *** AT4G00290.1 Mechanosensitive ion channel protein PF00924: Mechanosensitive ion channel IPR006685: Mechanosensitive ion channel MscS; IPR010920: LSM domain; IPR011014: Mechanosensitive ion channel MscS, transmembrane-2 GO:0016020 CC: membrane;GO:0055085 BP: transmembrane transport G PF00924 IPR006685; IPR010920; IPR011014 GO:0016020; GO:0055085

ESM_8 : Box plot distributions of F_4 according to their allele combinations at the two main FHB resistance loci for each of the three populations based on BLUEs of FHB severity in field (AUDPC) calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations of FHB severity in field (AUDPC) and plant height (cm) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.



	2B+ Fhb1+	2B+ Fhb1-	2B- Fhb1+	2B- Fhb1-	ddw1-wt Fhb1+	ddw1-wt Fhb1-	Ddw1-mut Fhb1+	Ddw1-mut Fhb1-	7A+ Fhb1+	7A+ Fhb1-	7A- Fhb1+	7A- Fhb1-
Number of lines	14	7	16	10	32	31	10	16	8	25	10	36
AUDPC mean	218^{de}	257^{bcde}	284^{bcd}	357^{ab}	251^{cde}	291^{bc}	333^{ab}	394^{a}	192^{e}	193^{ecc}	227^{cde}	242^{cde}
AUDPC sd	61	67	60	65	48	59	90	60	28	61	54	68
Height mean	122^{bc}	121^{bc}	122^{bc}	120^{bc}	133^{a}	129^{a}	104^{d}	102^{d}	118^{bc}	122^{b}	114^{c}	119^{bc}
Height sd	5	6	6	7	5	6	5	8	6	8	7	7

ESM_9 : Promising FHB resistant lines with their allelic composition for the 4 QTL with major effect on the FHB resistance mapped on chromosome 3B, 5R, 2B and 7A, and complementary phenotyping information on their plant height and FHB resistance level.

		Allelic compostion				BLUE overall year		
Pop	Name	3B	5R	2B	7A	PlantHeight	Severity in field (AUDPC)	Severity on grain (WKS)
T	K07_142	A	-	A	-	115.88	162.25	1.66
T	K07_178	A	-	A	-	125.25	165.94	1.64
T	K07_5	A	-	A	-	118.50	167.63	1.32
AG	K08_117	A	A	-	-	137.25	199.66	1.57
AG	K08_118	A	A	-	-	142.88	130.33	1.61
AG	K08_69	A	B	-	-	113.00	263.38	2.17
E	K09_4	B	-	-	A	114.13	151.46	1.89
E	K09_49	A	-	-	A	110.38	147.14	2.10
E	K09_59	B	-	-	A	146.25	97.59	2.08

The Allele 'A' originates from the common parent G8.06

The QTL detected on chromosome 3B mapped to marker positions *GWM493* and *GWM533* which flanked the position of the introgressed *Fhb1* locus from hexaploid wheat.

The QTL detected on chromosome 5R mapped to marker positions *Xiac129* and *Xiac130* which flanked the dwarfism gene *Ddw1*.

The QTL detected on chromosome 5R, 2B, and 7A were cross specific

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Figure 3 Box plot distributions of F_4 according to their allele combinations at the two main FHB resistance loci for each of the three populations based on BLUEs of FHB severity on grain (WKS) calculated across all experiments. Medians are indicated by solid lines, points represent outliers. For each subgroup, the number of lines, mean values and standard deviations of FHB severity on grains (WKS) and plant height (cm) are indicated. Values followed by different letters are significantly different ($p < 0.05$) based on Tukey test performed on each population independently.p72

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Abbreviation

ANOVA Analysis of variance

AG G8.06 x (F1: Agostino x Grenado)

BLUES Best linear unbiased estimator

DNA Deoxyribonucleic acid

DON Deoxynivalenol

E G8.06 x El Passo

FDK Fusarium-damaged kernel

FHB Fusarium head blight

GBS Genotyping-by-sequencing

LOD Logarithm of odds

LSD Least significant difference

MAS Marker-assisted selection

PAV Presence/absence variation

PH Plant height

QTL Quantitative trait loci

RIL Recombinant inbred line

SNP Single nucleotide polymorphism

SSR marker Single sequence repeat or microsatellite marker

T G8.06 x Tulus

WKS Whitened Kernel Surface

DECLARATION

Ich erkläre eidesstattlich, dass ich die Arbeit selbständig angefertigt, keine anderen als die angegebenen Hilfsmittel benutzt und alle aus ungedruckten Quellen, gedruckter Literatur oder aus dem Internet im Wortlaut oder im wesentlichen Inhalt übernommenen Formulierungen und Konzepte gemäβ den Richtlinien wissenschaftlicher Arbeiten zitiert, durch Fuβnoten gekennzeichnetbzw. mit genauer Quellenangabe kenntlich gemacht habe.

Orléans, November 2019