MASTER THESIS

Transgenerational defense induction for Fusarium head blight resistance in durum wheat

Submitted by
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Declaration on oath

I herebey declare in lieu of oath that I have composed this thesis on my own and without any inadmissable help from outside. I have not used any outside sources without declaration in the text. Any concepts or quotations applicable to these sources are clearly attributed to them.
This master´s thesis has not been submitted in the same or substantially similar version, not even in part, to any other authority for grading.

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List of abbreviations

AUDPC	Area under disease pressure curve
BLUEs	Best linear unbiased estimates
BYDV	Barley yellow dwarf virus
B3	Assessment number 3
DNA	Desoxyribonucleic acid
DON	Deoxynivalenol
FHB	Fusarium head blight
GS	Genomic selection
Hoh	Hohenheim
LSD	Least significant difference
NIV	Nivalenol
Oli	Oberer Lindenhof
PAMP	Pathogen-associated molecular patterns
PH	Plant height
PSVs	Phenotypically selected variants
WSMV	Wheat streak mosaic virus
ZEN	Zearalenone
ZGS	Zadoks growth stage

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Abstract

Durum wheat, with a worldwide production of 33 million tons per year is one of the most important cereals, thus it is necessary to improve the resistance properties of the crop.
Durum wheat is highly susceptible to Fusarium head blight (FHB). Classical breeding techniques like introgressing resistance quantitative trait loci (QTL) from related species into durum wheat were successfully carried out. The aim of this study was to investigate whether the selection for FHB resistance under Fusarium infection pressure can improve the resistance level of the offspring compared to the parental lines. Therefore, 17 durum wheat varieties were exposed to FHB disease pressure; the most resistant heads per variety were selected and advanced to the next generation. After three cycles of selection, the 25 most resistant heads per durum variety were harvested, seeds multiplied and tested for their FHB resistance together with the initial varieties. Field trials were performed at three locations with two replications each. One trial in Tulln, Austria, one in Hohenheim and one at the location Oberer Lindenhof, the latter two located in southwest Germany. Three preceding generations, the ancestors of those plants, were artificially inoculated at the University of Hohenheim with the fungus *Fusarium culmorum* to activate the innate immunity of the plants. The remaining undamaged grains were then used for the field trails. To test the resistance traits, the plots were artificially inoculated via backpack sprayers or conventional field sprayers in intervals of two to three days. To ensure good conditions for the fungus to infect the flowering plants, a mist irrigation system was set up, which frequently moisturised the plants before and while flowering. To measure the severity of FHB, the plots were frequently visually evaluated. Also, other traits like plant height and the date of flowering were noted. Within two varieties, Buck Candisur and Byblos, phenotypically selected variants (PSVs) could be identified which differed significantly from their initial variety in terms of FHB severity. In terms of plant height, PSVs from five varieties differed significantly from their initial varieties, consisting of the varieties Buck Candisur, SZD3048, Joyau, Fabulis and Byblos. Some of the PSVs descending from the variety Byblos, were both, more FHB resistant and taller compared to the initial variety. Further experiments are needed to confirm the assumed genetic background of the PSVs and to study epigenetic effects. However, the low number of significantly more resistant PSVs compared to the initial varieties suggests that epigenetic effects are of minor importance for FHB resistance in durum wheat.

Zusammenfassung

Durumweizen, mit einer weltweiten Produktion von 33 Millionen Tonnen pro Jahr, gehört zu den wichtigsten Getreidearten, daher ist es unerlässlich die Resistenzeigenschaften dieser Kultur zu verbessern. Durumweizen ist hoch anfällig für Ährenfusariose (Fusarium head blight, FHB). Klassische Züchtungsmethoden wie beispielsweise die Introgression von Resistenz-QTLs von verwandten Spezies in das Durum-Genom wurden bereits erfolgreich durchgeführt. Das Ziel dieser Studie war zu untersuchen, ob die Selektion auf FHB Resistenz unter Fusarium Infektionsdruck zu einer Erhöhung des Resistenzlevels der Nachkommenschaft im Vergleich zu den Elternlinien führen kann. Dazu wurden 17 Durumweizensorten einem FHB Krankheitsdruck ausgesetzt. Die resistentesten Ähren wurden selektiert und zur nächsten Generation auserkoren. Nach drei Zyklen wurden die 25 resistentesten Ähren pro Sorte geerntet, die Samen vermehrt und auf deren FHB Resistenz im Vergleich zu den initialen Sorten untersucht. Feldversuche wurden an drei Standorten mit je zwei Wiederholungen durchgeführt. Ein Versuch in Tulln, Österreich, einer in Hohenheim und einer am Standort Oberer Lindenhof, die letzteren beiden befanden sich in Südwest Deutschland. Drei vorangegangenen Generationen wurden an der Universität Hohenheim mit dem Pilz *Fusarium culmorum* künstlich inokuliert, um die angeborene Immunität der Pflanzen zu aktivieren. Die verbleibenden unversehrten Samen wurden für die Feldversuche verwendet. Um die Resistenzeigenschaften zu testen wurden die Parzellen künstlich mit Rückenspritzen oder konventionellen Feldspritzen in Intervallen von zwei bis drei Tagen inokuliert. Um zu gewährleisten, dass der Pilz gute Bedingungen zur Infektion vorfindet, wurde eine Sprühnebelanlage installiert, welche die Pflanzen in regelmäßigen Abständen vor und während der Blüte befeuchtete. Der Schweregrad der FHB wurde bestimmt indem in regelmäßigen Abständen die Plots visuell evaluiert wurden. Ebenso wurden Pflanzenhöhe und Blühdatum festgehalten. Innerhalb zweier Sorten, Buck Candisur und Byblos wurden phänotypisch selektierte Varianten (PSVs) identifiziert, die sich signifikant von den initialen Sorten hinsichtlich FHB Schweregrad unterschieden. Hinsichtlich der Pflanzenhöhe wurden fünf Sorten identifiziert, für welche PSVs sich signifikant von den initialen Sorten unterschieden, darunter die Sorten Buck Candisur, SZD3048, Joyau, Fabulis und Byblos. Einige der PSVs, abstammend von der Sorte Buck Candisur, waren sowohl FHB resistenter als auch länger im Vergleich zur Ausgangssorte. Weitere Experimente sind nötig, um den genetischen Hintergrund der PSVs zu bestätigen und um epigenetische Unterschiede zu analysieren. Die geringe Anzahl an signifikant resistenteren PSVs im Vergleich zu den

initialen Sorten legt jedoch nahe, dass epigenetische Effekte für die FHB-Resistenz von Durumweizen von untergeordneter Bedeutung sind.

1 Introduction

1.1 Wheat

1.1.1 Wheat and its importance

All wheat species (*Triticum*) are members of the grass family (*Gramineae*). Together with barley (*Bordeum vulgare*) and rye (*Secale cereale*), it is a member of the *Hordeae* tribe. These are also related to some weeds and wild grasses, which can be crossed with wheat. These Gramineae are often referred to jointly as *Triticeae* (Bozzine, David and Natoli, 2016).

Worldwide wheat is – based on annual production and consumption figures - the second most important grain crop. Based on projections of the United Nation's Food and Agricultural Organisation (FAO), global consumption in 2020 is estimated at 763 million tons, while for maize, the estimate is 1.444 million tons and for rice 512 million tons (FAO, 2020b).

From 1994 to 2018, the global production of wheat has increased from 525 million tons to 734 million tons, whereas harvested area – whilst displaying some fluctuations over these two and a half decades – has actually slightly decreased from 214,6 million ha to 214,3 million ha, as can be seen from Figure 1.

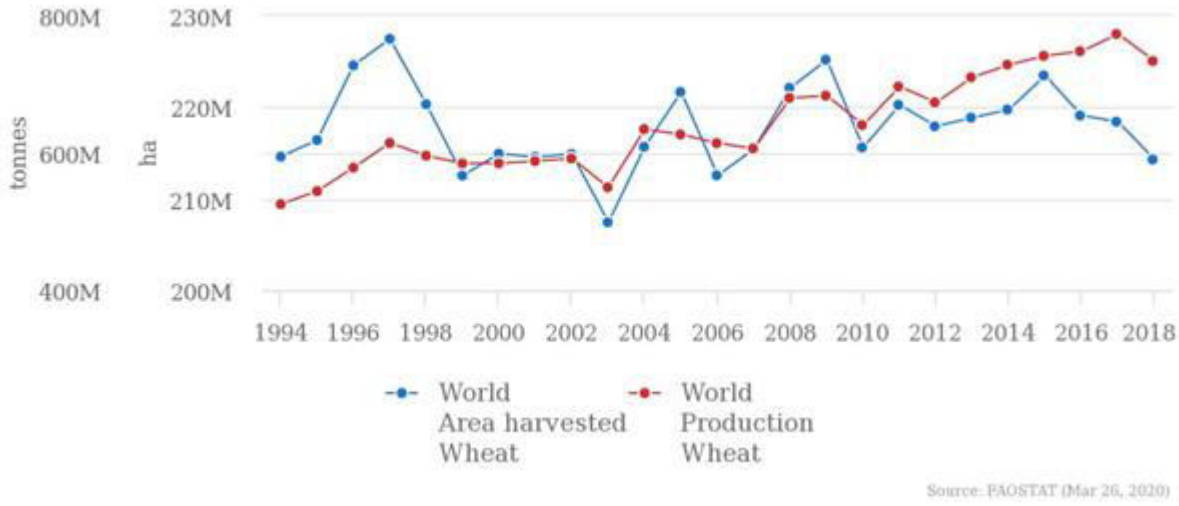


Figure 1: *Global Production/Yield quantities for Wheat (FAO, 2020a).*

The two curves depicted in Figure 1 indicate a markable increase in productivity from 2,4 tons / hectare in 1994 to 3,4 tons / hectare in 2018.

Within the 1994 – 2018 period, the most important production region for wheat has been Asia, with a global share of 43.6 %, followed by Europe with 32.6 % and the Americas, with 17%. In Oceania and Africa, only minor shares of global wheat harvest are produced, with 3.4 % and 3.3 % respectively (FAO, 2020a).

At a country level, for 1994 – 2018 the most important producer has been China with an annual production of 112 million tons, followed by India with 78 million tons, the USA with 58 million tons, the Russian Federation with 48 million tons, France at 36 million tons, Germany and Australia each with 22 million tons, Pakistan with 21 million tons and Turkey with 20 million tons, as shown in Figure 2.

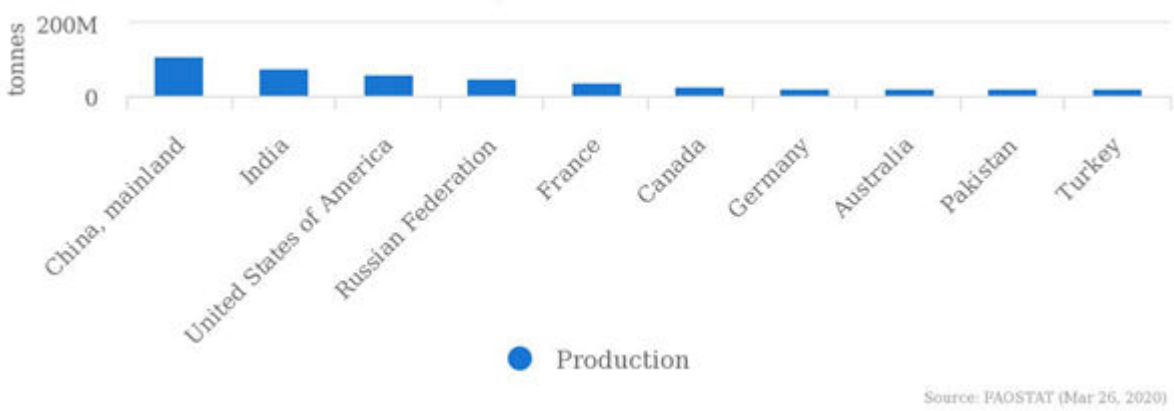


Figure 2: *Most important wheat producers (FAO, 2020a).*

Apart from the countries shown in Figure 2, Ukraine has become increasingly important in global wheat production over the last decade. If only the numbers from 2010 to 2018 are considered, Ukraine is ranked 10th amongst global wheat producers, if the time period is shortened to 2015 – 2018 Ukraine ranks 7th with an average annual production of 26 million tons (FAO, 2020a).

1.1.2 Durum wheat

While 95 % of global wheat production is made up by common or bread wheat, roughly 5 % is durum wheat, which is used to produce foods such as pasta or couscous. Hard wheat is characterised by having a hard kernel. Flour made from durum wheat is specifically high in its gluten content, thus rich in protein. Soft wheat is characterised by low gluten- and thus protein content and the resulting flour is typically used for products such as bread, cakes or biscuits (Oleson, 1994; Smith, 2017).

Durum wheat (*Triticum turgidum, subsp. durum*) is a subspecies of *Triticum turgidum*, which is a tetraploid wheat species (Bozzine, David and Natoli, 2016).

Archaeological records show that modern durum wheat was cultivated in Egypt during the periods of ancient Greece and Rome. It replaced tetraploidspecies such as emmer (*Triticum dicoccum*) from around 2300 BC. Today, durum wheat is cultivated on 10% of all wheat-cultivated areas, which makes it the most widely cultivated tetraploid wheat species. The remaining 90 % production areas are cultivated with hexaploid bread wheat species (Bozzine, David and Natoli, 2016).

Because wheat originates from regions with a dry climate, potential future drier climate conditions in its main growing regions are considered to have less of an impact on yields compared to other staple grains such as rice or maize (Daryanto, Wang and Jacinthe, 2016). However, scenario studies have shown that more than 50 percent of current growing areas will be affected in a negative way by climate change, with regions in South- and South-Eastern Asia, Eastern Europe and Russia likely to suffer a 20 percent decrease in yield. Conversely, for 20 percent of current growing areas, mostly in Eastern and Western Asia, South and Western Europe, the Western United States and the Andean region, future climate change is expected to result in more favourable conditions, resulting in yield increase of 20 percent or more. Across all growing regions these effects will result in a net decrease between 7 percent and 12 percent by the 2050s to 2090s (Balkovič et al., 2014).

1.1.3 Global Durum wheat production

Durum wheat is cultivated in semi-arid regions, using only rain for watering. It grows well in climates with cool nights and hot days during the growing season. In the Mediterranean regions of Southern Europe, Asia, and Africa, 60% of global durum wheat is produced. Spain, Italy, and Greece account for 80% of the total EU harvest. Globally, Canada is the most important producer with production located mostly in the prairie region. Canada is also an

important exporter of durum wheat. In the United States, the Great Plains are the most important production regions for durum wheat. The major limiting factor for durum wheat is water. Rainfall in winter is required for successful cultivation. Durum wheat requires precipitation levels of 200 – 600 mm annually. In the Mediterranean region, durum wheat is planted in late September to October and harvested in the early summer. In the North American regions, planting is carried out in April to May and the crop is harvested from August to September (Grant, Di Fonzo and Pisante, 2016).

As mentioned above, Canada is one of the most important producer and exporter of durum wheat, representing 60% of all exports with an annual average harvest of 4.2 million tons (Ranieri et al. 2016). The most important European exporter of durum wheat is France, with an annual production of two million tons (Ranieri et al., 2016). An overview of global export and import balances for durum wheat is provided in Figure 3. Data are for the 2005 – 2008 period (Ranieri et al., 2016).

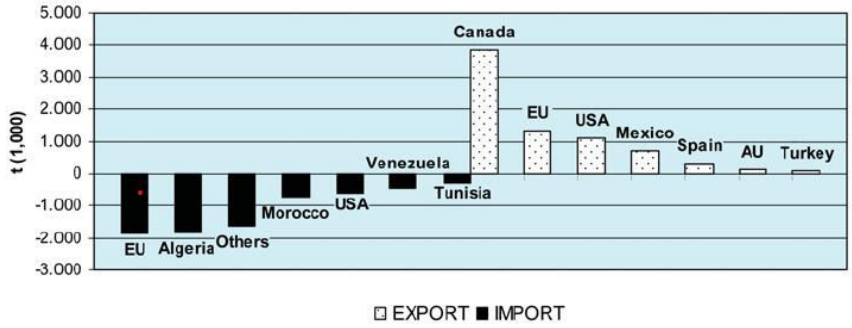


Figure 3: *Export/Import balances for main importing and exporting countries and regions (Ranieri et al., 2016).*

1.2 Fusarium head blight

There are many fungi species known in the genus *Fusarium,* which are the pathogens causing Fusarium head blight (FHB), also called scab (McMullen, Jones and Gallenberg, 1997). The disease can lead to massive losses in yield and quality of all cereal plants in almost all cereal growing areas. The complex of *Fusarium spp.* contains of more than 16 species (O'Donnell et al., 2004) and up to 17 organisms have so far been found responsible for FHB (Parry, Jenkinson and McLeod, 1995; Saharan et al., 2015). The pathogens *Fusarium graminearum, F. culmorum F. poae* and *F. avenaceum* are the most common species worldwide (Parry, Jenkinson and McLeod, 1995). *F. graminearum* is the most important agent for durum wheat causing FHB worldwide (Beccari et al., 2017; Leplat et al., 2013). In southern and eastern Europe, the USA, Canada and China *F. graminearum* is the dominant agent of FHB, whereas *F. culmorum* is the most important pathogen causing FHB in northern Europe (Gale, 2003).

1.2.1 Life cycle and disease progress of FHB

The disease progress of FHB can happen very fast. Rainfall, high humidity and dew while flowering until the kernel development period can promote the infection (McMullen, Jones and Gallenberg, 1997). Precipitation of 5 mm per day and temperatures of over 25 °C increases the risk of infections (Mesterházy, 2003). The earlier the fungus enters the host, the higher the damage in amount of yield, but if the pathogen infects the ears after flowering, the risk of a higher accumulation of mycotoxins increases (McMullen et al., 1012).

All *Fusarium* species are ascomycetes and they are the anamorphs of the genera *Gibberella* and *Nectria* which represent their teleomorphic stages (Schroers et al., 2011). *Fusarium* fungi are soil-borne facultative parasites which can survive on dead plant material. All *Fusarium* fungi form spindle-shaped or sickle-shaped conidiospores (Kück et al., 2009). In order to hibernate or survive dry phases, the fungi have survival strategies such as the formation of chlamydospores, thickened hyphae or perithecia (Saharan et al., 2015). Chlamydospores, macroconidia and the mycelium can be formed by *F. graminearum* (Sutton, 1982). Perithecia and ascospores are formed by the teleomorph *Gibberella zeae* (Dufault et al., 2007). To date no teleomorph has been found for *F. culmorum* and *F. poae* (Gale, 2003).

The sexually formed ascospores together with the asexually formed macroconidia are responsible for the spread within the cereal stocks and the main source of infection (Dufault et al., 2007). To date it is known that *F. culmorum* only spreads asexually via conidiospores. Chlamydospores are formed to survive long phases (Miedaner, 2012).

The largest proportion of infectious spores reach the leaves via splashes of rain where no symptoms occur but asexually spores (conidiospores) are still formed (Miedaner, 2018). This allows spores to get translocated more than 60 cm high and 100 cm wide, which leads to rapid increasing infection and spread of the inoculum within a cereal stock, especially for short growing varieties (Buerstmayer, Adam and Lemmens, 2012). It is not possible for the pathogens to penetrate the glume, palea and lemma of flowering wheat plants, the thick epidermal cell wall prevents them (Kang and Buchenauer, 2000). Pritsch et al. (2000) showed that after 5 to 6 hours macroconidia begin to germinate when they were placed on agar or wheat glumes. These germ tubes can quickly overgrow the surface of florets and glumes. Under favourable conditions, the mycelium can become thick enough to be seen by the naked eye (Bushnell, Hazen and Pritsch, 2003). When the mycelium overgrows the glume and the florets it finds portals of entry which are in most cases the stomata. Furthermore, the cleft between lemma and palea can represent ports for the fungus (Lewandowski and Bushnell,

2001). However, to date it remains unknown how and where germinating macroconidia penetrate the epidermis (Leonard and Bushnell, 2003).

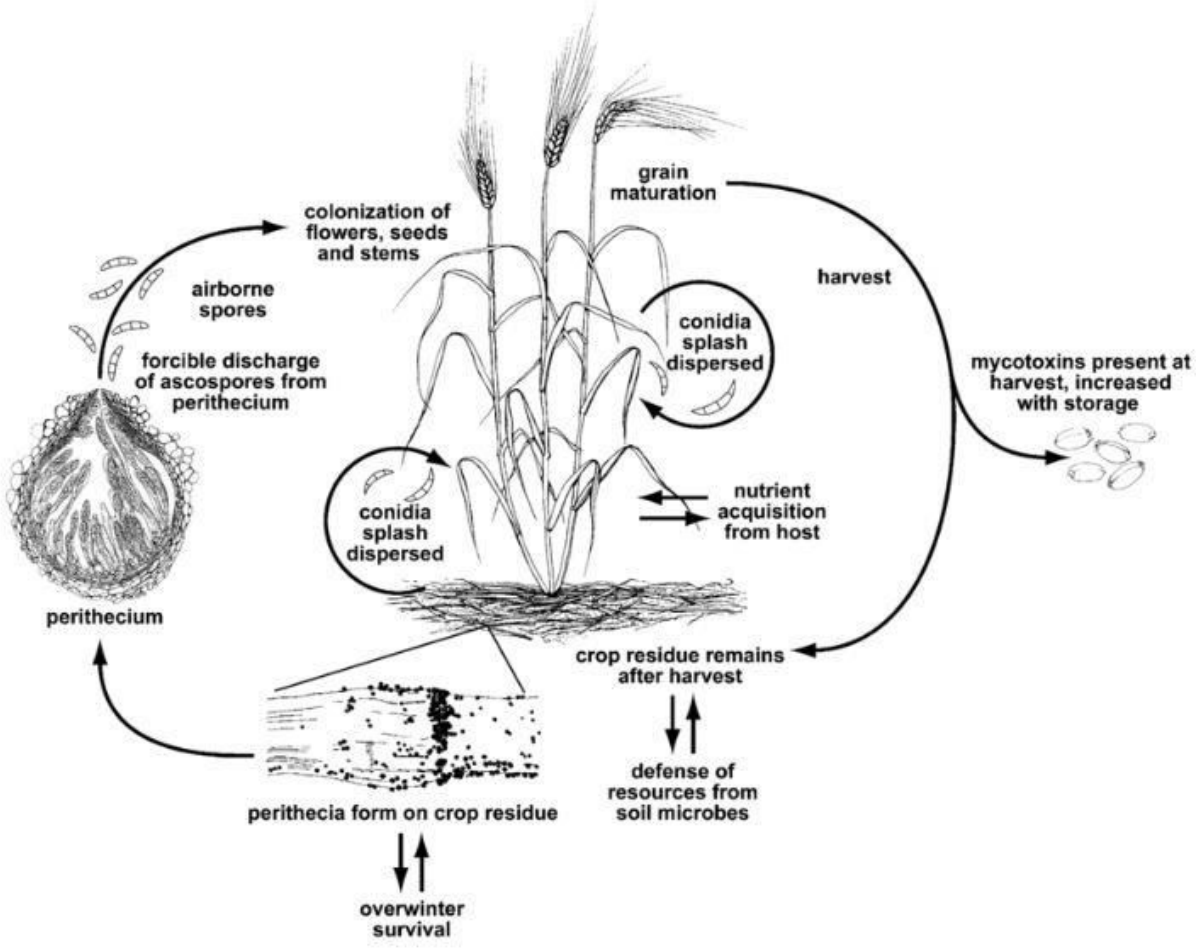


Figure 4: *Disease cycle of FHB (Trail, 2009)*

1.2.2 Symptoms

F. culmorum as well as *F. graminearum* infect all distal parts of grasses. In the case of *F. graminearum* beside the asexual life cycle the teleomorphic state can be formed. On crop debris or especially on maize stubbles, small, spherical, black perithecia can be seen (origin of asci with ascospores). In spring, when humidity is favourable, the ascospores are released. Via rain splashes or wind, the spores reach the ears where wilting symptoms become noticeable after the hyphae stop the water and nutrient supply of the spikelets. When humidity and temperatures increase, the salmon-pink mycelium on the edges of glumes and florets become visible, sometimes also at the nods of the rachis, a conspicuous characteristic of *F. graminearum* and *F. culmorum* (Miedaner, 2018; Saharan et al., 2015; Oldenburg and Ellner, 2015; Brown et al., 2010). The first symptoms of FHB become visible two to four days after infection. Small brown lesions are formed on the lemma which appear under moist conditions

such as on water-soaked spots (Kang and Buchenauer, 2000). On the developing caryopsis, dark brown spots become visible which spread until the whole kernel changes colour and can be covered by a white or pink mycelium, frequently grains with a lower mass and a crumpled appearance are formed (Bushnell, Hazen and Pritsch, 2003; Shaner, 2003). If the infection occurred accompanied by high inoculum amounts and before kernel development, often no grain will be developed at all (Bai and Shaner, 1994). After about two weeks, scattered bleached spikelets can be seen. As the disease progresses, single spikelets or top parts of the ear can fade and die back when the mycelium migrates into the vascular tissue of the rachis (Miedaner, 2018; Parry, 1990).

Figure 5: D*isease symptoms on a progressed stage.*
Top part of the ear is bleached out.

Figure 6: *Shows healthy ears of durum wheat.*

1.2.3 Mycotoxins

All FHB causing fungi produce mycotoxins except for *Microdochium nivale* (Miedaner, 2018), mycotoxins are secondary metabolites, which are produced by fungi and serve a variety of functions. They play a fundamental role in the transition of the pathogen from a biotrophic to a necrotrophic mode of life (Mirocha, Xie and Filho, 2003). Due to the phytotoxic effect, mycotoxins contribute significantly to the pathogenicity of the fungi (McCormick, 2003). On infected plants, in most cases, more than one mycotoxin can be found since most fungi are able to produce a few toxins and often infected plants are parasitized by more than one *Fusarium* species (Bottalico, 1998; Mesterhazy et al., 2005). Examples of secondary metabolites produced by *Fusarium* species are the following: trichothecenes, modified trichothecenes, fumonisins and fusarins, enniatins, culmorins and molecules such as zeralenone and moniliformin (Savard and Blackwell, 1994). The most

common and thus the most important structural groups of toxins produced by *Fusarium spp*. are trichothecenes, zeralenones and fumonisins (Bottalico, 1998). Mycotoxins are not only a problem in human consumption but also an issue in livestock farming. The name vomitoxin was given to deoxynivalenol (DON) by swine growers who drew a connection between the consumption of fusarium-infected corn with emesis (vomiting). Swine which are fed with mycotoxin containing corn refused it (Mirocha, Xie and Filho, 2003). Charmley et al. (1995) pointed out that up to 25% of all cereal products worldwide are contaminated with mycotoxins. Eriksen and Alexander (1998) said that for a few mycotoxins like DON this percentage can be even higher.

1.2.4 Trichothecenes

The mycotoxin DON received the most attention regarding to identification, not least by the fact that, DON and nivalenol (NIV) are the most frequent and most important mycotoxins. With a ketone at C-8, DON is also called 8-ketotrichothecen and belongs to group B trichothecenes as well as NIV (Mirocha, Xie and Filho, 2003). *F. graminearum* in the southern parts of Europe and *F. culmorum* in the northern parts are the most important producers of DON and NIV, while the group A trichothecenes to which the toxins HT-2 and T-2 belong are mainly produced by *F. poae* and *F. sporotrichoides* (Miedaner, 2018). Common among the group A trichothecenes is the ester bond at C-8 (Mirocha, Xie and Filho, 2003). In most cases DON is found in infected seeds. In contrast, the highly toxic A trichothecenes can be identified less frequently (Cerón-Bustamante et al., 2018). Recently, Kelly et al. (2015) and Varga et al. (2015) identified a new A trichothecen in Canada and the USA which is called NX-2. Trichothecenes are inhibitors of protein synthesis, hence they are highly phytotoxic. It has been assumed that the synthesis of defensive proteins is inhibited by the toxins. The toxic effect appears in the form of chlorosis, necrosis or wilting symptoms (Lemmens *et al.,* 2005). Trichotecenes represent a strong virulence factor. McCormick (2003) showed in an experiment with *F.graminearum,* in which the biosynthesis pathway for trichothecenes was blocked, that they were still as pathogenic as the wild type but less virulent. The spreading from the place of infection through the ear was however inhibited in the mutants.

1.2.5 Other important mycotoxins

Besides some of the trichothecenes like DON and NIV, zearalenone (ZEN) is of high importance in livestock farming and food safety (Bottalico, 1998). The main effect of ZEN is caused by its' oestrogenic characteristic. ZEN and its metabolites bind to oestrogen receptors which was shown by studies using monkeys and rodents (Fuller et al., 1982; Kuiper-Goodman, 1987). The fungus appeared to interfere with the reproductive system. Bacon, Robbins and Porter (1977) showed strong correlation between the amount of ZEN produced and formation of perithecia. Also, Wolf, Lieberman and Mirocha (1972) provided evidence that suggests a possible linkage. The consumption of ZEN-containing products leads to decreased fertility and abortion. Swine react most sensitively to these mycotoxins (Miedaner, 2018; Bottalico, 1998). Buxton (1927) was the first to describe the oestrogenic effect in swine. He reported about uterotrophic reactions after the consumption of moulded corn. *F. graminearum* and *F. culmorum* rank among the main producers on ZEN (Bottalico and Perrone, 2002).

Like ZEN, fumonisins are often found on maize worldwide, and are mainly produced by *F. moniliforme* and *F. proliferatum* (Bottalico, 1998; Marasas et al., 2001). Eriksen and Alexander (1998) reported that in most cases, healthy looking corn contain higher concentrations of fumonisins that moulded cobs. The most common types of fumonisins are fumonisin B_1 and fumonisin B_2. Two fatal disease are triggered by these mycotoxins, the equine leucoencephalomalacia in horses, where the white part of the cerebrum is affected. Also, necrotic lesions form and the liver can retain damage. The second disease is called Porcine Pulmonary Oedema Syndrome and occurs in swine. Consumption of contaminated feeds by pigs can result in dyspnoea, cyanosis, weakness and death (Bottalico, 1998; Marasas et al., 2001). Furthermore, there is evidence that fumonisins can lead to kidney and liver damage and even cancer in rats. In humans, ingestion can lead to oesophageal cancer (Eriksen and Alexander, 1998).

Other mycotoxins are fusaric acids, moniliformin, wortmannin, fusarochromanone and fusaproliferin. These toxins are less relevant from an economical point of view, as they occur less frequently and some were just identified recently. However, some of these metabolites are highly toxic (Bryden et al., 2001). Especially moniliformin was described by Cole et al. (1973) as highly toxic. In contrast, fusaric acids are not as toxic, but there is evidence that it can act as a synergist alongside other mycotoxins (Bryden et al., 2001). Bacon, Porter and Norred (1995) showed in a study conducted on fertile chicken eggs, that the toxic effect of fumonisin B_1 was increased when fusaric acid was present. Moniliformin was firstly found in

1973 produced by *F. moniliforme* in infected maize (Cole et al., 1973). Main producers are *F. moniliforme* in maize and *F. avenaceum* in wheat (Battilani et al., 2009). Plants react very sensitively to moniliformin and show symptoms of poisoning. It is therefore assumed that it contributes to the pathogenicity of the producer (Cole et al., 1973).

1.2.6 Countermeasures

It has been observed that recently *Fusarium* species such as *F. graminearum* occur more often in colder regions of Europe, which makes the establishment of effective countermeasures indispensable even in northern growing regions (Xu et al., 2008).

Success can be achieved through management strategies such as resistance breeding, crop rotation, tillage or the use of fungicides. Even biological control agents such as bacteria or competitive fungi have shown promising results (Schisler, 2002). However, one method alone only brings moderate benefits (Paul et al., 2008).

Because fungicides, in case of FHB, are mostly inefficient and can lead to ecological problems, one of the best ways to deal with the issue is in the progress and application of plant breeding i.e., the development of resistant varieties (Buerstmayr, Ban and Anderson, 2009). For common hexaploid wheats auspicious FHB resistance sources have already been identified, but this is not the case for tetraploid durum wheats (Kumar et al., 2007). Therefore, other approaches should be reviewed.

1.2.7 Fungicides against FHB

The treatment with fungicides in commercial agriculture is a key factor to minimize the symptoms and contamination of wheat grains with mycotoxins (Mesterházy et al. 2011).

The most common and licensed active ingredients are triazole associated products, which are also the most successful fungicides in controlling FHB especially tebuconazole. Others are metconazole, propiconazole and prothioconazole (Wegulo et al. 2015; Mesterházy, 2003). Other active agents are strobilurines, azoxystrobin, mancozeb, prochloraz, triadimenol, methoxyacrilat and numerous others (Mesterházy, 2003).

For optimal results, the application time point is critical. Active agents like triazoles and strobilurins do not get relocated from the site of contact to the heads. Too early applications protect the leaves, but emerging heads are weak points. First applications should be performed after all heads have emerged. Furthermore, the rate and selection should be chosen, the

weather conditions and the application technique are main factors to achieve satisfactory results (Mesterházy, 2003).

Fernandez et al. (2012) showed that an application with tebuconazole at the earliest stage of flowering results in lowest FHB symptoms and highest kernel weight compared to an application between stem elongation and flag leaf emergence. But double fungicide application between Zadoks growth stage (ZGS) 31 or 37 and ZGS 60 with the same active agent did not show improved results in terms of FHB symptoms or higher yields. Also, Blandino, Minelli and Reyeri (2006) pointed out that a fungicide treatment at a late growth stage in this case, mid anthesis results in higher yields, lower FHB symptoms and lower mycotoxin values. Early applications like seed dressings or treatments at shooting are less effective against FHB.

Furthermore, Blandino, Minelli and Reyeri (2006) indicate that a mixture of azoxystrobin and a triazole can lead to higher mycotoxin values compared to the control. Also, D'Mello et al. (2001) showed a correlation between the presence of azoxystrobin and an increased production of DON by the fungus in vitro. Pirgozliev et al. (2003) suggested with a field study that the active agent promotes *Fusarium* infections indirect by reducing the presence of *Microdochium nivale.*

1.3 Resistance breeding

Attempts towards resistance breeding as a controlling measure against FHB date back to the late 19th century. For more than a century, until 1999, phenotype selection was the main method available (Steiner et al., 2017). In order to identify suitable lines to be combined in a breeding programme, indicators for FHB resistance need to be present in one of the two lines to be crossed (Buerstmayr, Ban and Anderson, 2009). Resistance against FHB needs then to be assessed in all lines of a breeding population. In order to arrange for homogeneous disease levels in all trials, artificial inoculation is required and disease-related indicators need to be assessed for all resulting lines (Steiner et al., 2017). The level of FHB infection can be assessed by visual observation of disease symptoms on wheat heads, the assessment of the percentage of diseased kernels by visual means, quantitative yield for the trial, assessment yield quality such as protein content and the measuring of mycotoxin content. In addition, morphological indicators for plant-pathogen interaction such as height, anther extrusion, compactness of wheat ears, flower opening and date of heading are assessed (Buerstmayr, Ban and Anderson, 2009). Out of the number of possible indicators for disease level, typically

disease incidence, severity of disease and post-harvest kernel assessment are used in trials (Steiner et al., 2017).

With the development and improvement of molecular genetics, it became possible to determine resistance to FHB through the identification of quantitative trait loci (QTL) in QTL mapping studies for hexaploid wheat (Anderson et al., 2001). The identification of stable and large effect QTL and of markers strongly linked to these effects enable marker-assisted selection. *Fhb1, Fhb2, Fhb4, Fhb5, Fhb7, Qtfhs.ifa-5a, Qtfhs.nau-2DL* are the major FHB resistance QTL (Steiner et al., 2017). Comparison between phenotypic selection and marker-assisted selection have shown both methods to be equally successful for the selection of lines with the highest levels of resistance and a combination of both methods, with initial phenotypic selection followed by marker-assisted selection has been suggested (Agostinelli et al., 2012). In practical breeding in North America, *Fhb1* is predominately used, as well as less frequently *Qfhs.ifa-5A,* whereas in Europe due to the preference for native resistance sources, thus far, only the variety Jaceo (Syngenta Seeds) carrying *Fhb1* has resulted from breeding programmes (Steiner et al., 2017). Available methods for QTL mapping are linkage mapping and genome-wide association studies. For both methods, there exists a significance threshold for genomic signals derived from markers, beyond which marker effects drop to a level at which they cannot be considered in the analysis (Arruda et al., 2016).

Beside phenotypic and marker-assisted selection, the third approach in resistance breeding is genomic selection (GS). Through the estimation of genome-wide marker effects simultaneously for many markers within a phenotyped population, these can be used to predict estimated breeding values for non-phenotyped individuals within a breeding population and allows for preselection of lines for more cost-intensive phenotype selection tests, resulting in shorter breeding cycles (Steiner et al., 2017). In an analysis of 2325 European soft winter wheat lines, GS models displayed high accuracy for the prediction of FHB resistance, leading to the conclusion that GS would be a promising strategy for breeding programmes focusing on native resistance sources (Mirdita et al., 2015). GS models with improved accuracy could be selected more efficiently by focussing on subsets of training population lines and markers. This could be implemented through the development of genotyping platforms for marker subsets rather than genome-wide techniques (Hoffstetter et al., 2016).

1.3.1 Resistance genes

Most work related to the identification of FHB resistance genes in wheat has been focused on the hexaploid source Sumai 3, for which the presence of two to three resistance genes has been suggested (Bai and Shaner, 1994; Bai, Xiao and Mei, 1989). In this context, additive effects are considered to be higher than non-additive effects, from which it has been concluded that an enhancement of resistance could result from an accumulation of resistance genes from a variety of sources (Bai and Shaner, 1994).

In addition, the variance in resistance to FHB is also considered to be influenced by environmental factors, which increases the complexity of this trait and could be at the same level as that for the trait of grain yield (Campbell and Lipps, 1999).

In order to analyse resistance against FHB in tetraploid wheat, Tunisian lines have been the subject of research efforts related to the identification of FHB resistance genes in durum wheat in studies conducted by Ghavami et al., 2011 or Elias et al., 2005.

1.3.2 FHB resistance in Durum wheat

FHB resistance in durum wheat has become increasingly important in recent decades due to climate change, the introduction of more susceptible short genotypes as well as agronomic practices such as conservation tillage practices, resulting in increases of splash-dispersed and stubble-borne diseases. Given the importance of durum wheat for human nutrition, even achieving adequate levels of tolerance rather than higher or full resistance is thus considered to be a rewarding objective for resistance breeding programmes in durum wheat (Fernandez and Knox, 2016).

While considerable successes have been achieved in resistance breeding against FHB in hexaploid wheat, the application of similar approaches in durum wheat were facing considerable challenges, which led to speculations about possible resistance suppressors present in durum wheat. The major challenge for FHB resistance breeding in durum wheat is the fact that durum wheat shows only low levels of genetic variation (Prat et al., 2016).

The reason of this lack of variation has not yet been clarified. One explanation could be that modern durum wheat varieties descends from germplasm which was cultivated preferably in warm and dry Mediterranean regions where the infection pressure was not relevant (Ban et al., 2005). Another reason could be that the investment in breeding programs were higher for bread wheat which resulted in a lower variation of genetic resources available for *T. durum* (Oliver et al., 2008). Recently the QTL *Fhb1* has been introgressed successfully into durum

wheat from hexaploid wheat. The FHB resistance in three durum wheat crosses between the *Fhb1* harbouring experimental *T. durum* line – DBC-480 and three European *T. durum* varieties was significantly increased (Prat et al., 2016). Prat (2016) also identified chromosome arms 2BL, 4AL, 4BS, 5AL and 6AS as genomic regions associated with FHB resistance by genotyping with SSR and genotyping by sequencing. DBC-480 was found to contribute resistant alleles at all loci, while the effect of *Fhb1* in the context of FHB resistance was also verified by evaluating type II resistance in one out of the three populations used in that study.

This resulted in lines with higher FHB resistance levels. In this study, a strong effect of the *Rht-B1* locus in reducing FHB severity was identified. The resulting breeding lines were considered to be close to modern European germplasm as regards agronomic characteristics (Prat et al., 2016).

Five moderately resistant Tunisian wheat lines have also been identified by Elias et al., (2005). More distantly related and some wild relatives of durum wheat were also investigated for their FHB resistance. However, none of these shows a comparably high level of FHB resistance as identified in hexaploid wheat (Steiner et al., 2017).

In China, breeding programmes have been successful in the selection of a few moderately resistant lines of durum wheat (Pehlken and Kalverkamp, 2019).

Forte et al. (2014) focused on traits linked to $7el_1L$ and $7el_2L$, pyramiding these derived from *Thinopyrum ponticum* into durum wheat. The resulting $7el_1L$ and $7el_2L$ tetraploid durum lines were proven to exhibit 70 percent to 80 percent reduction in FHB severity following inoculation. These lines also displayed good agronomic performance.

Furthermore, *T. dicoccoides* is a promising source of resistance alleles also for durum wheat (Nevo, 2014). The resistance accessions Israel A, denoted *Qfhs.ndsu-3AS* was already verified in two durum wheat varieties and contributed to an increase of resistance up to 50% for homo- and heterozygous genotypes (Soresi et al., 2017).

1.4 Epigenetics as an alternative approach

Since durum wheat is highly susceptible to FHB and due to the low genetic variation within the species, classical breeding techniques are hampered (Prat et al., 2016). Thus, alternative approaches are needed. Because focussing on a single genetic trait such as FHB resistance is not possible, a systemic approach was developed in Brazil and Canada concurrently, which aimed at developing a holistic understanding of the plant's genetic system and its interactions

with the environment, while also giving considerations to agronomical practices as well as customer demands (Comeau et al., 2011).

Such changes in the reactions of plants to their environment can be achieved by changing their epigenetic (Haber et al., 2011). Epigenetic is defined by the covalent changes of the DNA and the histones attached to it, without changing the sequence itself. Such changes are the methylation, demethylation or hydroxy methylation of the DNA also methylation, acetylation and phosphorylation of the histones can alter the expression of genes (Iwasaki and Paszkowski, 2014). Also, small RNAs are known to activate or block the expression of genes, thus the process is classified as epigenetics (Jiao and Slack, 2014). In breeding programs based on epigenetics, plants are exposed to various stress factors at levels which may potentially damage the plant but not kill it before seed set. Transgenerational induction of plant defence mechanisms against stress are constituted by changes in gene expression, the production of defence signalling hormones and the production and accumulation of defence-related end products. Small molecules as phloem-mobile small RNA are transferred from vegetative tissue to developing seeds. By repeating stress treatment in subsequent generations and the analysis of response behaviour, potentially stronger or more rapid response behaviour by an offspring of exposed maternal plants can be assessed in comparison to an offspring of undamaged control plants (Holeski, Jander and Agrawal, 2012). The concept is depicted in Figure 9.

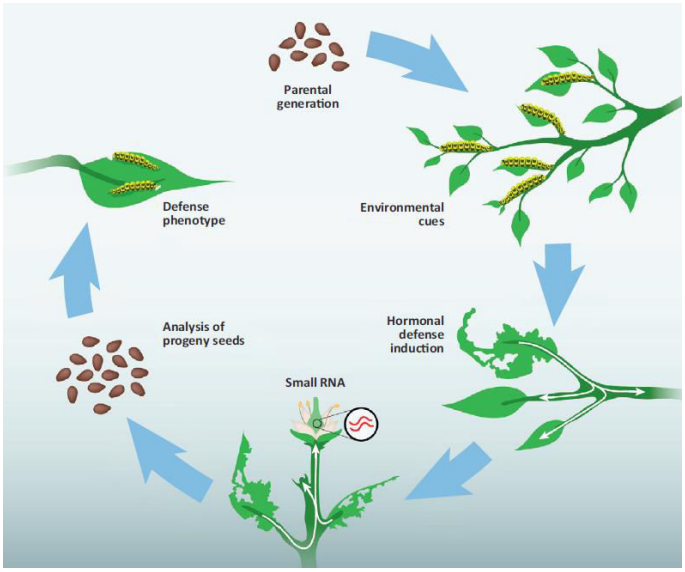


Figure 9: *Schematic of the steps involved in transgenerational induction (Holeski, Jander and Agrawal, 2012).*

Plant immune responses against pathogens include physiological phenomena such as the closure of stomata to limit penetration of pathogens, the production of reactive oxygen species and nitric oxide, the reduction of nutritional transfer from cytosol to apoplast, callose deposition as well as biosynthesis of antimicrobial metabolites and defence hormones such as salicylic acid, jasmonic acid and ethylene. In coevolutionary history, pathogens have developed means to suppress plant immune responses. These are proteins translocated into plant cells, affecting protein or gene activity, yet plants defy these using transmembrane as well as intracellular receptors detecting these effectors (Ramirez-Prado et al., 2018).

Epigenetic manipulation, as described above, is the appropriate method for plant breeding to provide the desired variations with regards to abiotic and biotic stress factors, without manipulation of the DNA sequence. Given the growing demand for food as well as reductions of per capita land and water as well as increasing climate related stress both as regards direct impact on temperature and precipitation regimes as well as indirect impact through increased spread of diseases and pests, the approach allows for the arrival at lines resistant to stress as well as showing desired agronomic traits (Kumar, Singh and Mohapatra, 2017).

The main reasoning behind the epigenetic approach is that the exposition to stressful environments, plants can develop rapid-response strategies to cope with stress based on existing genes. The evolution of such mechanisms is thus epigenetic by definition. Plants are considered to have developed such mechanisms of evolution, since without a means to escape environmental stress (Haber et al., 2011).

The systemic approach mentioned above is based on combining the impact of various diseases. Comeau et al. (2011) used a combination of barley yellow dwarf virus (BYDV) and Fusarium. Tolerance to BYDV is coupled with higher yield and while the virus also increased FHB damage, the objective was to arrive at lines with good agronomic performance as well as improved resistance. In addition to BYDV and FHB, other stress factors were also applied in the breeding programme throughout different growth development stages. The Selection was done in the F_1 generation, within which only one cross showed satisfying performance in FHB- as well as BYDV tolerance and seed appearance. A multi-resistant AB143 line resulted in the F_6 generation in which one group of plants had good Fusarium resistance. Half of lines from that group showed lower DON content than Sumai 3. Further breeding with crosses of AB143 and varieties named Kingsey, Nass, Duo or AW625 (varieties with valuable levels of FHB resistance) resulted in higher frequencies of more tolerant progenies (Comeau et al., 2011).

Epigenetic breeding programmes can also result in lines displaying traits not present in ancestral plants. These so called *de novo* traits have been identified in a large scale breeding

research programme focusing on Wheat streak mosaic virus (WSMV) resistance. In this programme, resistance to leaf rust, which could then also be conferred to lines from parents susceptible to WSMV were identified. However, undesirable traits such as progressive necrosis emerged in some lines resulting from that programme. It was thus concluded that the wheat genome contains information for useful traits, not expressed in current plants (Seifers et al., 2014).

1.4.1 Innate immunity

Much knowledge has already been gained in classical methods of plant breeding (Paterson, Freeling and Sasaki, 2005). However, in this time there is not much known about the epigenetic mechanisms and in its heredity in agricultural plants while in the model organism *Arabidopsis thaliana* there has been a lot of research work in this topic. Nevertheless, the intensity of the linkage between the phenotype and the epigenetic variation is still not understood (Nordborg and Weigel, 2008). Epigenetic processes like DNA methylation have important tasks in epigenetic regulation of the transcription. Also processes like demethylation and hydroxy methylation may feature epigenetic regulation. These are covalent modifications of the DNA. As well as the DNA, also histones can be altered by covalent modifications like acetylation, phosphorylation, methylation and others (Iwasaki and Paszkowski, 2014).

Since plants do not have an immune system which operates in the same way as e.g. the one of mammals, they respond in another way to attacks by pathogens. The penetration of a pathogen triggers a cascade of reactions in plants, allowing it to respond with a defence strategy. It is enabled by the plant innate immunity (Ramirez-Prado et al., 2018). One well known mechanism of plants immunity reactions is the recognition of pathogen-associated molecular patterns (PAMPs) by pattern-recognition receptors in the plant cells. This is described as the first layer of the innate immune system of plants and is pertaining to as PAMP-triggered immunity (Zipfel 2007).

However, the transgenerational memory of plants grown under infection-pressure which leads to permanent stress is a new topic of research. Some studies have indicated that defence-induced epialleles can be transmitted vertically and can be stable over years (Haber et al., 2011; Ramirez-Prado et al., 2018). Since it is not clear if infection-pressure by itself in only three cycles of generations can lead to a significant increase of FHB resistance to the offspring of those plants, the following research questions were investigated.

1.5 Research questions

This study concerns with the questions:

- Is there a vertically transmission of FHB resistance which extends over multiple generations from ancestors grown under infection pressure?
- How do the durum wheat varieties behave in terms of FHB resistance compared to each other?

2 Materials and methods

2.1 Plant material

2.1.1 Durum varieties

Seventeen varieties and breeding lines of spring durum wheat were used for carrying out the trials. The varieties were chosen to cover a wide range from highly susceptible to moderately susceptible to FHB.

Table 1: *Varieties/ breeding lines used for the study. For blank cells no scientific characterisation was available (Jentsch and Günther, 2017, Soresi et al., 2017, Kling and Münzing, 2009, Cirlini et al., 2014, Trottet et al., 2014).*

Variety/ breeding line	Country of origin	FHB susceptibility
Duramonte	Spain	low
Joyau	France	low
Buck Candisur	Argentina	moderate
Karur	France	moderate
Neodur	France	moderate
Byblos	France	high
Miradoux	France	high
Pescadou	France	high
Wimadur	Germany	high
Durafit	Germany	
Fabulis		
Nefer	France	
Radur	Germany	
Ramirez		
AO138-rz01		
SZD 3048	Austria	
2.076/04/01		

2.1.2 Selection of PSVs per variety

In 2014 at the University of Hohenheim the 17 durum varieties were sown sparsely in about 0.2 m² plots and inoculated with *F. culmorum*. Via a conventional field sprayer, the plants were inoculated when 50 % of the plants of one plot were flowering. Then every second to third day the plots were sprayed to perform the inoculation at the best possible time. This procedure was repeated till two days after 50% of the plants from the last plot were flowering. After the kernels reached maturity the healthy ears were marked harvested by hand. Only healthy seeds were used for the next season to repeat this process twice in 2015 and 2016. For the trials in 2017 seeds were multiplied from the 24 most resistant ears per variety representing the 24 phenotypically selected variants (PSVs) for each variety.

2.2 Field experimental sites

2.2.1 Location Tulln

One test site was located in Tulln an der Donau, in Lower Austria on fields of the University of Natural Resources and Life Sciences (BOKU), at the Department of Agrobiotechnology IFA Tulln. The trials were conducted in the region Tullner Becken, which is approximately 48 km long and about 14 km broad at the widest point (boku.at.ac). Coordinates of the test site were 48°19’ N and 16°04’E (google maps). The altitude is about 180 m above sea level. Tulln is at the intersection of two climate zones, the central-european-ozeanic climate and the pannonian-continental climate (boku.ac.at) with a mean temperature of 9.7 °C and a precipitation on average of 625 mm per year (climate-data.org). In Figure 1a the monthly mean temperature and the total amount of precipitation per month is shown for the location Tulln. With a mean temperature of 10.0 °C, in 2017 it was slightly higher than the long-term observation from 1982 to 2012. The precipitation with a total amount of about 486 in 2017 fell far below the long-term observation which is 625 mm (climate-data.org). The rainfall in the time of flowering to ripening of the ears from Mai to end of June were less than the normal conditions, especially in June with a usual amount of almost 70 mm (see figure 10a).

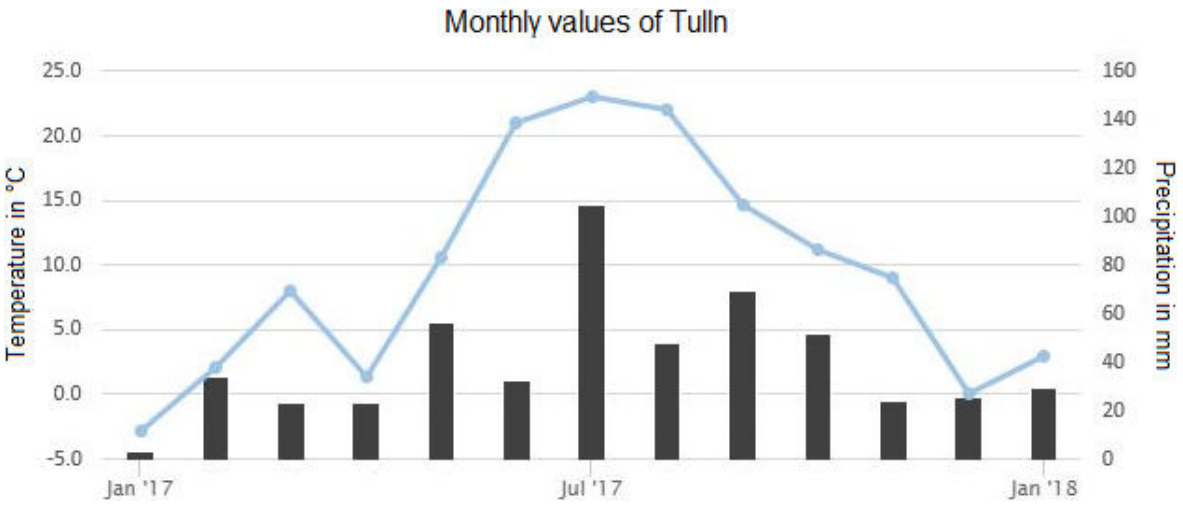


Figure 10a: *Climate chart of location Tulln for the Year 2017. The black bricks indicate the total amount of precipitation in mm of one month, the blue curve shows the mean temperature in °C per month (Universität für Bodenkultur Wien, 2019).*

2.2.2 Location Hohenheim

At the University of Hohenheim (Hoh), Department of Plant Breeding, a second trial was carried out with the same parameters as those of Tulln. The test site is located near Stuttgart in the south of the "Neckarbecken" in Baden-Württemberg. Coordinates are 48°42'50" N and 9°12'58" E. The climate is of central-european-ozeanic character (Landeshauptstadt Stuttgart, Amt für Umweltschutz, 2018). The total amount of precipitation per year is 685 mm and the mean temperature is 8.5 °C at approximately 400 m above sea level (University of Hohenheim, 2017). The soil type is defined as a loess-based stagnic Luvisol with silty-loam nature. In the Figure below the mean temperature of the year 2017 is visualised. The average of the temperature with 10.1 °C in the year 2017 was much higher than in the long-term observations. The total amount of rainfall was much more in 2017 with 844 mm. In the growing period from sowing to flowering which was April to June the precipitation was higher in total, except for Mai where it was a bit less.

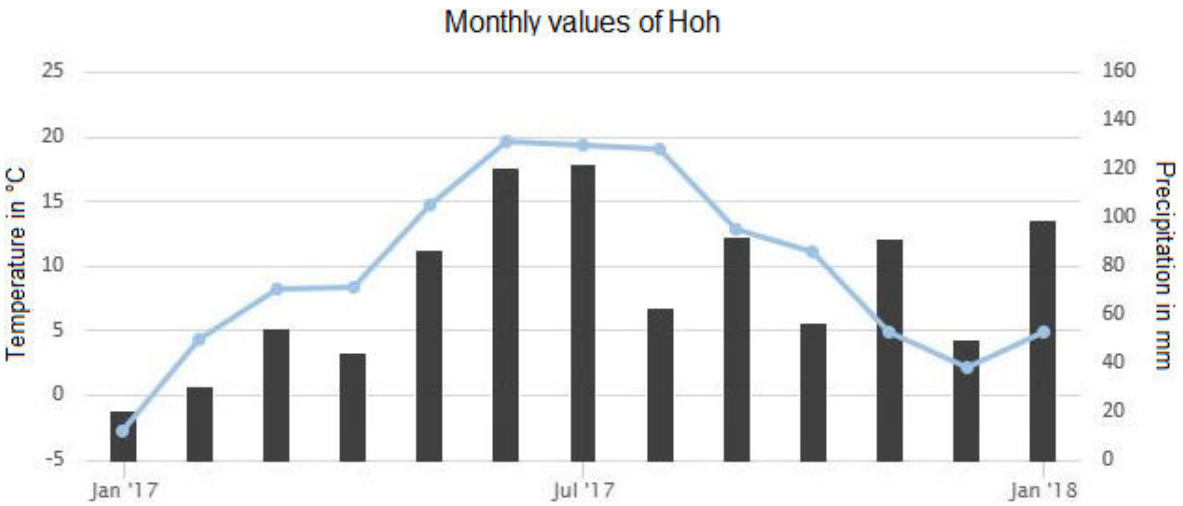


Figure 10b: *Climate chart of location Hoh for the Year 2017. The black bricks indicate the total amount of precipitation in mm of one month, the blue curve shows the mean temperature in °C per month (Wetterstation Hohenheim, 2019).*

2.2.3 Location Oberer Lindenhof

The third trials were conducted at the location Oberer Lindenhof (Oli), which is a test area of the University of Hohenheim. It is approximately 30 km south of Hohenheim. The Coordinates are 48°28'26" N and 9°18'17" E (google maps 2019) at a sea level of about 700 m and the mean temperature of 6.9 °C (Wang, Gruber and Claupein, 2013). The total annual precipitation was 942 mm measured from 1970 to 2010. Oberer Lindenhof belongs to the Swabian Alb mountains in Baden-Württemberg in south-west Germany (ibid.). The climate still temperate-oceanic but with less temperatures and more precipitation. The type of soil is a Cambisol with a silty loam-nature (Galiano-Carneiro et al., 2019). In total the rainfall was in 2017 with 817 mm less than in the mean of 1970 to 2010. It was even less then at the location Hoh. The mean temperatures of approximately 8.3 °C were higher in the year of the trials as in the long-term observations. The weather data of the months April to June can only be compared with data from Reutlingen which is about 8 km north-west to Oli because long-term data was not available. In April the precipitation was more in 2017 than in the average of the data. In May and June, the rainfall was less. The mean temperatures cannot be compared with those of Reutlingen due to the difference in altitude of about 320 m.

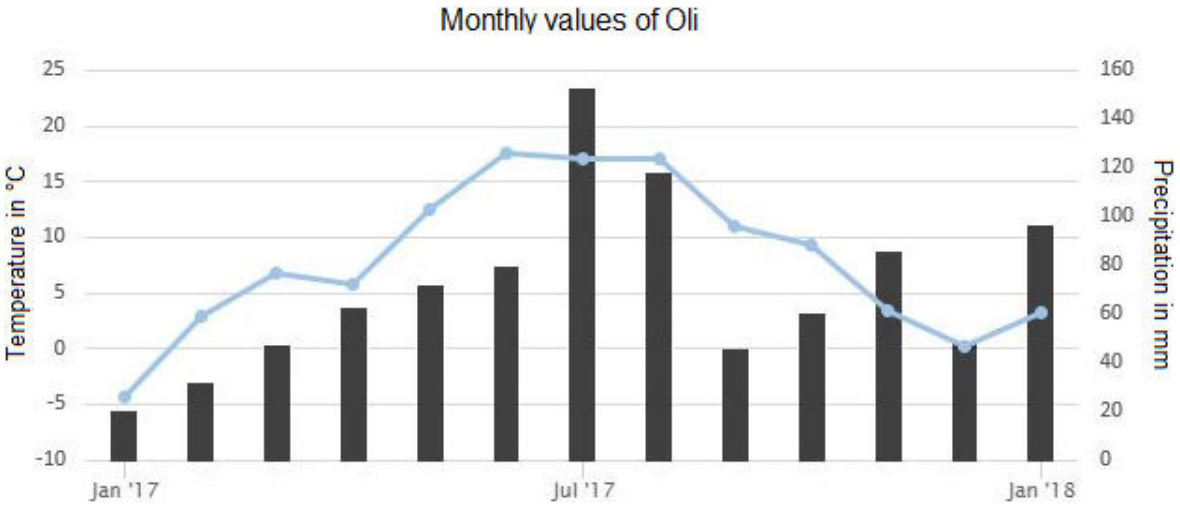


Figure 10c: *Climate chart of location Oli for the Year 2017. The black bricks indicate the total amount of precipitation in mm of one month, the blue curve shows the mean temperature in °C per month (Wetterstation Oberer Lindenhof, 2019).*

2.3 Experimental design and crop maintenance

All three experiments were sown in early spring with a few days between each replication. In Tulln, the date of drilling was March 13th 2017 for the first replication and March 16th 2017 for the second replication. Every trial consisted of two replications and in total of 50 blocks. Within each block 17 plots were planted. Each variety consisted of 24 PSVs and one initial variety except for the variety Byblos, consisting of 21 PSVs and the initial variety, and the Ramirez variety consisting of 23 PSVs and the initial variety. They were planted as an alpha lattice design. The plots were single rows and had a length of 65 cm. Between the plots the distance was 30 cm and between the rows 40 cm. The amount of seeds per plot was 2.5g.

All experiments were maintained in accordance with good agronomic practice. The experiments in Tulln were treated with the fungicides "Celest Trio©" and Latitude each with 2 ml/kg seeds as a seed treatment. "Celest Trio©" contains 25 g/L Difenoconazole, 25 g/L Fludioxonil and 10 g/L Tebuconazole, and the active ingredient of Latitude is 125 g/L Silthiofam. Two applications of herbicides were necessary, on May the 6. 2017 0,2 L/ha of the product "Arrat©" containing 250 g/kg Tritosulfuron and 500 g/kg Dicamba and 1 L/ha of the adjuvant "Dash©E.C." were applied. On May 30. 2017 1 L/ha of the herbicide "Puma Extra©" containing 63,6 g/L Fenoxaprop-P and 75 g/L Mefenpyr-diethyl was applied.

On April 4th 2017 a NPK (17:6:18 + 7S) fertilizer and on May 19th 2017 a calcium ammonium nitrate fertilizer, containing 27 % N, was applied. The previous crop was soybean.

2.4 Inoculum production

The production of the inoculum was done following the standard operation procedure (SOP-Code: 3-S-04-01) if the IFA Tulln.

A 50 g mixture of one part of oats and two parts wheat was filled in a small glass container (baby food glass) together with deionised water to let it swell over one night. After approximately 24 hours the excess water was then poured away, and the oat-wheat mixture was autoclaved for 20 min. at a temperature of 121 °C. At the same time, the *Fusarium* strain was scattered onto a SNA (special Nierenberg agar). The fungus grown on this agar was then used to inoculation the wheat-oat-mixture. The fungus strain used for this procedure was obtained from the microbial stem collection of the IFA.

The glass containers with kernels were then stored under diffuse light conditions for two weeks, after which they were overgrown by the fungus. The colour of the kernels turned to brown-orange. Once a day the glasses were shaken for better aeration. Following this, the mixture was stored at 4 to 8 °C in the refrigerator until further use.

To produce the inoculum of *F. culmorum*, the glass was filled with deionized water and was shaken well. Afterwards the mixture was poured through a sieve in a second vessel. The conidia in this solution were used for counting in a Bürker-Türk-counting chamber to determine the concentration. Following the formula C1 x V1 = C2 x V2 the desired concentration of 10^4 ml^{-1} was then calculated. To store the conidia until using they were filled in 10 ml tubes placed in the refrigerator at -80 °C.

2.5 Inoculation

The inoculation was performed when the first plot started flowering till end of flowering of the latest plot. Every second day the trial was inoculated using a backpack sprayer at the late afternoon to avoid high radiation during noon. One vial of macroconidia of *F. culmorum* was necessary for 10 l of water with a concentration of 12 500 conidia per ml. This concentration was lower in comparison to trials of soft wheat, due to the high susceptibility of durum wheat against FHB. The walking speed was adapted in that way that in total 10 ml of the spraying solution was given to one plot. To have good conditions for infection an irrigation system was set up which sprayed the field regularly on the day of inoculation till the next day.

2.6 Assessment of traits

2.6.1 FHB assessment

For assessing the FHB severity at the Tulln location, a scoring system depicted in Table 2 was used to display the severity in percentage. On 14, 28, 22 and 26 days after inoculation the assessments were carried out. In Hoh and Oli the assessments were conducted using a scale from 1 to 9 with 1 showing no symptoms, <5% of infected spikelets per plot is 2, 5-15% is 3, 15-25% is 4, 25-45% is 5, 45-65% is 6, 65-85% is 7, 85-95% is 8, >95% is 9 (Miedaner, Schneider and Oettler, 2006).

Table 2: *Instruction for the FHB scoring used in Hoh and Oli from 1 to 9 and Tulln in percent.*

scoring system in Hoh and Oli	% of diseased spikelets per plot	visually estimated average per plot
1	0	no visible symptoms
	0,1	first visible symptoms
	0,5	0.1 spikelets per ear infected
	1	0.2 spikelets per ear infected
	2	0.4 spikelets per ear infected
	3	0.6 spikelets per ear infected
2	5	1 spikelet per ear infected
	10	2 spikelets per ear infected
3	15	3 spikelets per ear infected
	20	4 spikelets per ear infected
4	25	5 spikelets per ear infected
	30	6 spikelets per ear infected
5 (25 - 45 %)	40	8 spikelets per ear infected
	50	10 spikelets per ear infected
6 (45 - 65 %)	60	12 spikelets per ear infected
	70	14 spikelets per ear infected
7 (65 - 85 %)	80	16 spikelets per ear infected
8 (85 - 95 %)	90	18 spikelets per ear infected
9 (> 95 %)	100	all spikelets per ear infected

2.6.2 Measuring of Plant height

After the last assessment, the plant height (PH) was measured using a measuring stick with marks in a five cm interval. The PH was recorded without awns in the middle of each plot.

2.6.3 Assessment of earliness

In Tulln the flowering date was recorded. As soon as 50% of the plants of a plot were flowering the date was noted. In Hoh the calendar day of heading was recorded and in Oli the BBCH stage on the 20th of June was noted. To compare the assessments of each location the records were fitted in a 1 to 7 scale with 1 indicating early flowering and 7 indicating late flowering plants.

2.7 Statistical analysis

2.7.1 AUDPC area under disease pressure curve

The AUDPC was calculated for the first three assessments (FHB B1, FHB B2 and FHB B3). The assessment four in Tulln was not included because in Hoh and Oli only three assessments were performed. The following formula was used for the calculation (The American Phytopathological Society, 2021):

$$A_k = \sum_{i=1}^{N_i-1} \frac{(y_i + y_{i+1})}{2}(t_{i+1} - t_i)$$

2.7.2 BLUEs Best Linear Unbiased Estimates

In this study the traits FHB at assessment number 3 (B3) and the area under disease pressure curve (AUDPC) as the traits for FHB severity, the plant height (PH) and the date of flowering (earliness) were used for the statistical analysis. As an incomplete block design was used- the checks, the initial varieties, and their PSVs were replicated between the replications but not between individual blocks. The BLUEs were calculated for each trait and for each location using the *sommer* package with the "mmer" function in the free software RStudio according to (Covarrubias-Pazaran, 2016).

The model used therefore was the following:

(1) $Y_{ijk} = \mu + G_i + R_j + GR_{ij} + \varepsilon_{ijk}$

Y_{ijk} value for the i^{th} genotype in the j^{th} replication for the k^{th} block
μ overall mean
G_i i^{th} genotype
R_j j^{th} replication
GR_{ij} genotype- replication interaction
ε_{ijk} error term

2.7.3 Heritability and repeatability

The repeatability and heritability were calculated with the model (1) and (2) using the *sommer* package of RStudio. For each location, the repeatability (H^2) was derived. The variance components were used for the calculation: σ2G denotes the genotypic variance and σ2E the error variance. For all locations together the broad-sense heritability (H^2) was calculated σ2GxL denotes for the genotype-location variance n indicates the number of locations and r the number of replications across the locations.

Repeatability was calculated using the model (1)

The following formula was used to calculate the repeatability:

$$H^2 = \frac{\sigma 2G}{\sigma 2G + \frac{\sigma 2E}{r}}$$

Broad-sense heritability:

(2) $Y_{ijk} = \mu + G_i + L_k + R_j + GL_{ik} + LR_{jk} + \varepsilon_{ijk}$

Y_{ijk} value for the i^{th} genotype in the j^{th} replication for the k^{th} block

μ overall mean

G_i i^{th} genotype

L_k k^{th} location

R_j j^{th} replication

GL_{ij} genotype- location interaction

LR_{jk} Location- replication interaction

ε_{ijk} error term

The following formula was used to calculate the broad-sense heritability:

$$H^2 = \frac{\sigma 2G}{\sigma 2G + \frac{\sigma 2GxL}{n} + \frac{\sigma 2E}{r}}$$

2.7.4 LSD and variance components

Also, the least significant difference (LSD) and the variance components were calculated using RStudio. For LSD, the package *agricolae* with the function "LSD.test" was used. For calculation of the variance components the *sommer* package was used. The following variance components were calculated using the model (2).

σ2Genotype
σ2Location
σ2Location-Replication interaction
σ2Genotype-Locaion interaction
σ2Error

2.7.5 Analysis of phenotypic data

To test the varieties and the replications against each other a Kruskal-Wallis test was performed. To analyse if significant differences between the individual PSVs and their initial varieties are present, Wilcoxon rank-sum tests were performed using R Studio.
The following model was fitted:

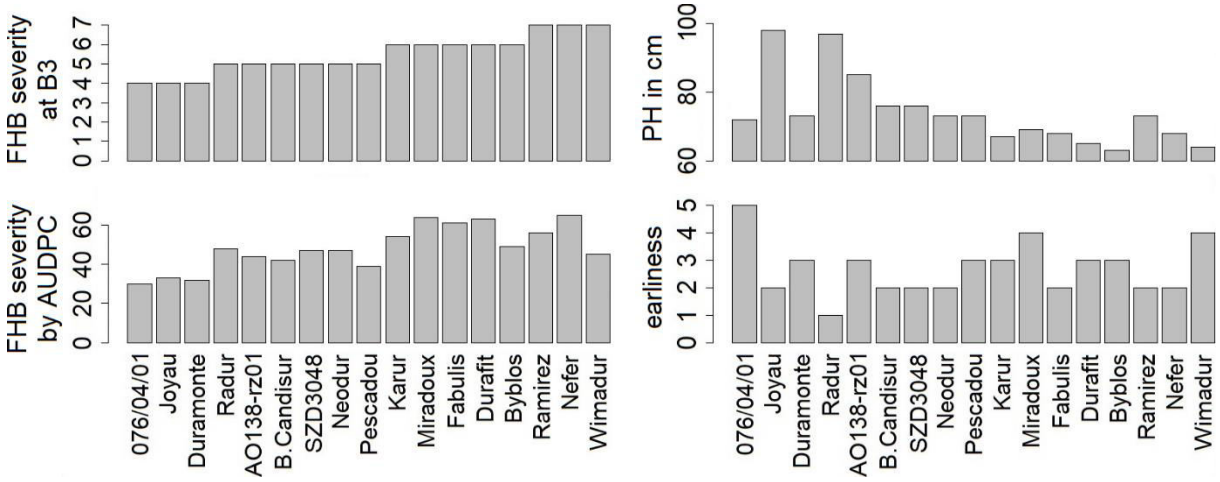
(3) $Y_{ij} = \mu + G_i + R_j + \varepsilon_{ij}$

Y_{ij} value for the i^{th} genotype in the j^{th} replication
μ overall mean
G_i i^{th} genotype
R_j j^{th} replication
ε_{ijk} error term

3 Results

3.1 FHB resistance, plant height and date of anthesis of the 17 initial durum varieties

The 17 durum wheat varieties and breeding lines showed a broad variation for FHB resistance as measured by FHB severity at rating No. 3 (B3) on a 1-9 scale and AUDPC, PH as well as earliness (Figure 11a to 11d). The varieties are distributed between 4 and 7 scale points for the trait FHB severity at B3. Ramirez, Nefer and Wimadur show the highest susceptibility with 7, whereas the breeding line 076/04/01 and the varieties Joyau and Duramonte reached the best resistance properties with 4. In general, the AUDPC data confirmed the results, the only differences can be seen between the varieties Nefer and Wimadur, which is however not significant in FHB data. The reason is the rapid disease development from low to high severities during the three assessments in Nefer, whereas in Wimadur the disease was already at a progressed stage at the time of the first assessment. In the PH-barplot there are three varieties which protrude. Radur and Joyau were the tallest varieties with about 100 cm followed by the breeding line AO138-rz01 with 95 cm on average. Joyau is also one of the three varieties with high resistance to FHB. The other two are moderately resistant. Shorter varieties are often more susceptible, like Durafit, Byblos, Nefer and Wimadur with a PH of about 70 cm on average. Despite the short PH of the breeding line 076/04/01 and the variety Duramonte, they show high resistance to FHB. On a scale from 1 to 7 with 7 indicating late flowering plants, the trait earliness is illustrated. Most varieties were categorized as early flowering (2 to 3 scale points). Radur was the earliest variety and revealed tall PH and moderate resistance to FHB. The latest flowering variety was the breeding line 076/04/01 followed by Miradoux and Wimadur. 076/04/01 showed high FHB resistance while Miradoux and Wimadur were susceptible to FHB.



Figures 11a, 11b, 11c and 11d: *Barplots of data distribution of the initial varieties for FHB severity at B3 (1= resistant, 9= highly susceptible) and AUDPC, PH in cm and earliness (1= early, 7= late flowering).*

3.2 FHB resistance, plant height and date of anthesis of the phenotypically selected variants

The histograms in Figure 12a to 12d reflect the phenotypic variation as observed for FHB resistance at B3 and AUDPC, PH and the trait earliness for the 404 PSVs, comprising 25 PSVs for each of the 17 initial varieties. Here, the data is not normally distributed for the trait FHB resistance at B3, PH and earliness. The data for FHB resistance measured by AUDPC, however, shows a normal distribution. There is a peak at about 45 and the data is slightly skewed to the left like the histogram for FHB severity at B3. There is a peak at about 4.5, in the middle of the histogram for FHB severity at B3, but the remaining data does not correspond to a Gaussian distribution. The data of PH is skewed to the left, towards short PH, as well as the earliness-data towards early flowering plants. Most PSVs were 65 and 70 cm tall, only a few were between 80 and 110 cm corresponding roughly to the data of the initial varieties. The same trend occurs for the earliness data. Most PSVs were early flowering, categorized with 2 to 3.5 on a scale from 1 to 7.

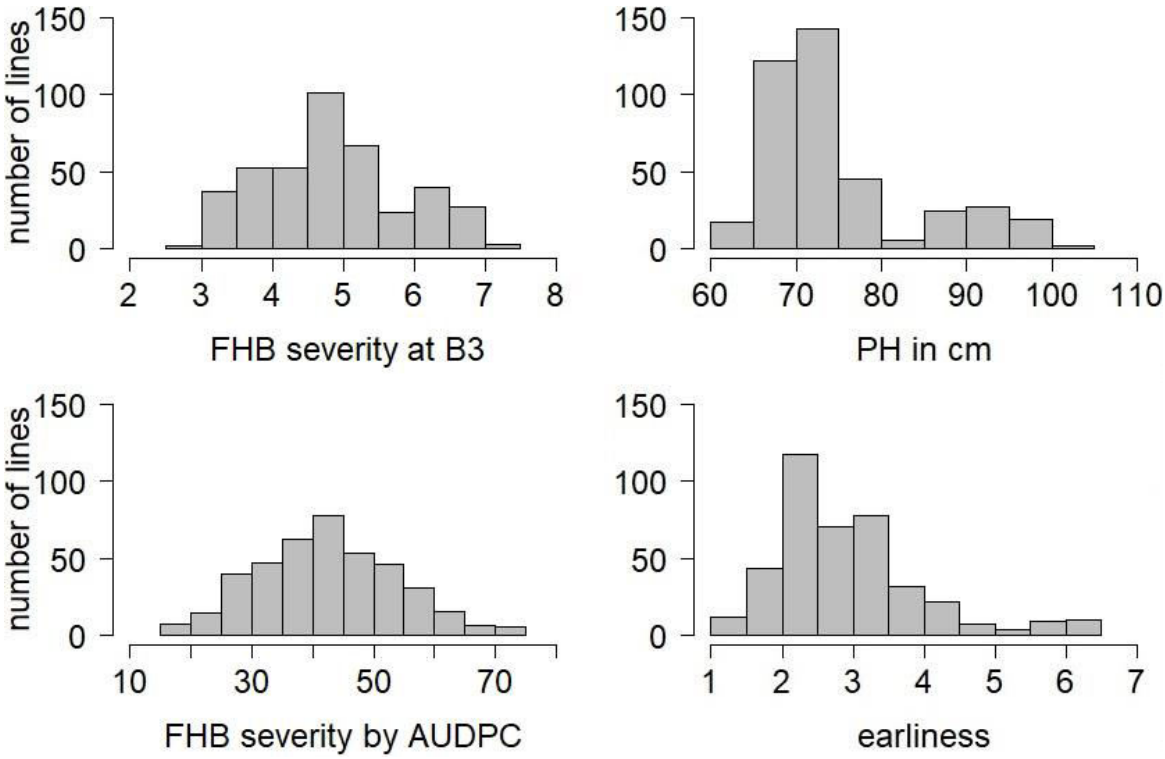


Figure 12a, 12b, 12c and 12d: *Histogram of the 404 PSVs for FHB severity at B3 and AUDPC, PH in cm and earliness of all locations, showing the estimated BLUEs.*

3.3 Variety effect of the 17 initial varieties and their PSVs

The results of Kruskal-Wallis tests are displayed in Table 3. For the calculation, the BLUEs for FHB severity at B3 and AUDPC over all locations was used. The results show significance for the FHB severity at B3 as well as FHB severity by AUDPC for the varieties.

Table 3: *Kruskal-Wallis test for varieties of all locations (Loc.), the BLUEs of the initial varieties and PSVs. Data descends from FHB severity at B3 and FHB severity measured by AUDPC. The p-value represents highly significance indicated by **, significance indicated by * or blanc for no significance.*

BLUEs of FHB B3 all Loc.	**chi-squared**	**df**	**p-value**
varieties	475.95	16	**
BLUEs of AUDPC all Loc.			
varieties	227.01	16	**

Table 4 shows the results of Kruskal-Wallis tests over all locations and each location separately between the varieties and the replications. The data used was FHB severity at B3 and FHB severity by AUDPC. At each location and at all locations together significance was

detected between the varieties. For the replications only for the FHB severity at B3 at all locations a significant value was calculated. Neither for FHB severity at B3 nor for FHB severity by AUDPC a significant effect was found at the Tulln location. For all other locations, a significance was calculated.

Table 4: *Kruskal-Wallis test for* varieties *and replications at all locations (Loc.) as well as location Tulln, location Hoh and location Oli, including initial varieties and PSVs. Data descends from the BLUEs of FHB severity at B3 and FHB severity measured by AUDPC. The p-value represents highly significance indicated by **, significance indicated by * or blanc for no significance.*

FHB B3 all Loc.	**chi-squared**	**df**	**p-value**
varieties	813.07	16	**
Replication	22.99	1	**
AUDPC all Loc.			
varieties	195.74	16	**
Replication	8.84	1	*
FHB B3 Tulln			
varieties	548.20	16	**
Replication	0.76	1	
AUDPC Tulln			
varieties	561.33	16	**
Replication	0.53	1	
FHB B3 Hoh			
varieties	453.81	16	**
Replication	20.92	1	*
AUDPC Hoh			
varieties	165.14	16	**
Replication	20.89	1	*
FHB B3 Oli			
varieties	431.41	16	**
Replication	19.22	1	*
AUDPC Oli			
varieties	135.24	16	**
Replication	4.29	1	*

3.4 FHB resistance properties of the initial varieties and PSVs on the individual locations

FHB resistance evaluations at the three locations are displayed in Table 5 for the FHB severity at B3. Means, minimum and median show higher FHB severities for the initial varieties in all locations compared to the PSVs. The maximum is one scale point higher for the PSVs in all locations. The PSVs show slightly higher resistance values on average except for the minimums at all locations.

Table 5: *Mean, maximum (Max), minimum (Min) and median of FHB at B3 of the 17 initial varieties (left number) and the 404 PSVs (right number) from the three locations (Loc.), Tulln, Hohenheim (Hoh) and Oberer Lindenhof (Oli).*

Initial varieties / PSVs	Loc. Tulln	Loc. Hoh	Loc. Oli
Mean	3.9 / 3.6	6.3 / 5.7	5.8 / 5.3
Max	6.0 / 7.0	8.0 / 9.0	8.0 / 9.0
Min	2.0 / 1.0	4.0 / 2.0	4.0 / 2.0
Median	4.0 / 3.0	6.0 / 6.0	5.5 / 5.0

Figure 13 shows the mean disease progress curve for the three locations for all tested initial varieties and PSVs. It can be seen that the varieties in Tulln started with lower disease symptoms. Overall, FHB severity in Hoh and Oli was similar over the three assessments. In Oli the curve flattened out after the second assessment, whereas in Hoh the curve increased as well as in Tulln.

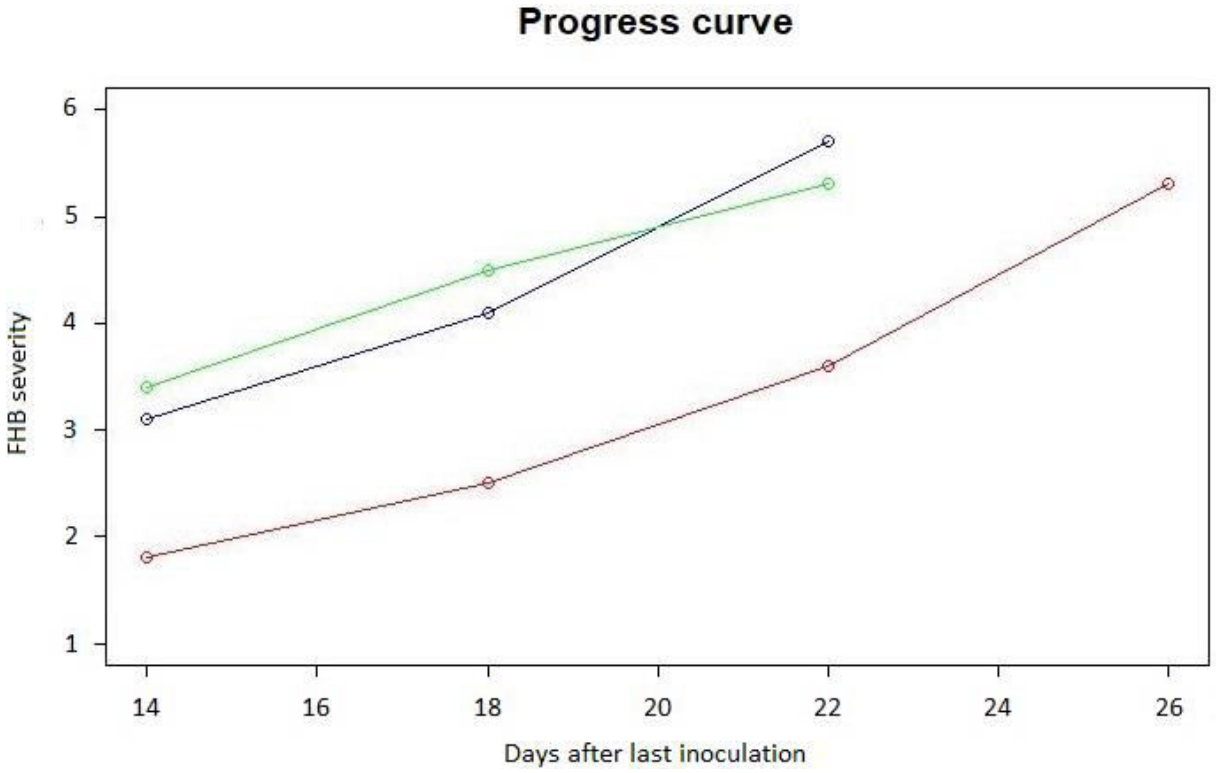


Figure 13: *Disease progress curve of the three locations of all lines including initial varieties and PSVs on average. The X axes indicates the days after last inoculation when the assessments were taken. The Y axis shows the FHB severity. Red curve is from dates of Tulln, blue from Hoh and green from Oli.*

3.5 LSD and variance components

Table 6 shows the results of the variance components and the LSD over all locations for the traits FHB severity at assessment B3 and AUDPC, PH and earliness. For the trait FHB severity the location effect ($\sigma^2_{Location}$ = 1.18) explains the largest part of the total variance. The location-replication interaction ($\sigma^2_{Location\text{-}Replication}$) contributed least for every trait. For AUDPC the error effect (σ^2_{Error}= 247.78) contributed most, even more than the location effect ($\sigma^2_{Location}$= 186.63) and the genotype-location interaction ($\sigma^2_{Genotype\text{-}Location}$= 143.29). The total variance for PH was high. The largest part of it was the genotype effect ($\sigma^2_{Genotype}$= 80.82). Location and error effect were almost equal ($\sigma^2_{Location}$= 28.23, σ^2_{Error}= 27.34).

Table 6: Variance components for genotype ($\sigma^2_{Genotype}$), location ($\sigma^2_{Location}$), location-replication interaction ($\sigma^2_{Location\text{-}Replication}$), genotype-location interaction ($\sigma 2_{Genotype\text{-}Location}$) residual effects ($\sigma^2_{Error}$), and the LSD for the traits FHB severity at B3 (FHB B3) and AUDPC, PH and earliness.

Variance components	FHB B3	AUDPC	PH	earliness
σ2Genotype	0.80	36.71	80.44	0.99
σ2Location	1.18	186.63	28.38	0.06
σ2Location-Replication	0.05	4.99	0.37	0.05
σ2Genotype-Location	0.35	143.29	3.49	0.17
σ2Error	0.56	247.78	24.85	0.38
LSD	1.54	25.74	7.98	0.90

3.6 Repeatabilities and heritabilities of the traits FHB severity at B3 and AUDPC, PH and earliness

The results for the repeatabilities and heritabilities are plotted in Table 7. For the FHB rating at B3 the calculation of repeatability derived H^2 =0.86 for Tulln, H^2 =0.85 for Hoh and H^2 =0.79 for Oli. For the AUDPC, H^2 are still high in Tulln (AUDPC =0.77), but lower for Hoh (AUDPC =0.46), and for Oli (AUDPC =0.42). For the trait PH, in turn, the repeatabilities are high very with (PH =0.95) for Tulln, (PH =0.92) in Hoh and (PH =0.82) in Oli. Also high earliness values were calculated for every location with (earliness =0.90) in Tulln, (earliness =0.96) in Hoh and (earliness =0.81) in Oli. The heritability was highest for the trait PH with (H^2 =0.94). For earliness with (H^2 =0.89), FHB B3 with (H^2 =0.79) and the least value with (H^2 =0.52) was calculated for the AUDPC.

Table 7: *Repeatabilities for each of the three locations Tulln, Hoh and Oli and broad-sense heritabilities for all locations together for the traits FHB severity at B3 and AUDPC, PH and earliness, for the initial varieties and their PSVs.*

	FHB B3	AUDPC	PH	earliness
H^2 Location Tulln	0.86	0.77	0.95	0.90
H^2 Location HOH	0.85	0.46	0.92	0.96
H^2 Location OLI	0.79	0.42	0.82	0.81
H^2 all locations	0.79	0.30	0.94	0.89

3.7 Comparison of the PSVs with their initial durum varieties for FHB resistance

Figure 14 shows boxplots of the 17 varieties and their 25 PSVs each for FHB severity. The FHB resistance data was derived from means over all locations. A Wilcoxon rank-sum test identified for two of the durum backgrounds significantly different PSVs. Two PSVs (E127 and E141) were significantly (p-value < 0.05) higher resistant than the initial variety Buck Candisur and even eleven PSVs for the variety Byblos: E337, E340, E342, E346, and E349 revealed significantly lower, the PSVs: E338, E341, E347, E350, E351 and E356 even highly significant (p-value < 0,01) lower disease severities compared to the initial variety. For four durum backgrounds initial varieties were more resistant than the median of the PSVs 2.076/04/01, SZD 3048, Joyau and Nefer, but there are no significant differences, see Figure 14. Within almost every variety both, more resistant and more susceptible PSVs were derived from the initial ancestors. Except for the varieties Radur, Karur, Buck Candisur, Joyau and Fabulis, where the initial lines showed the highest susceptibility to FHB.

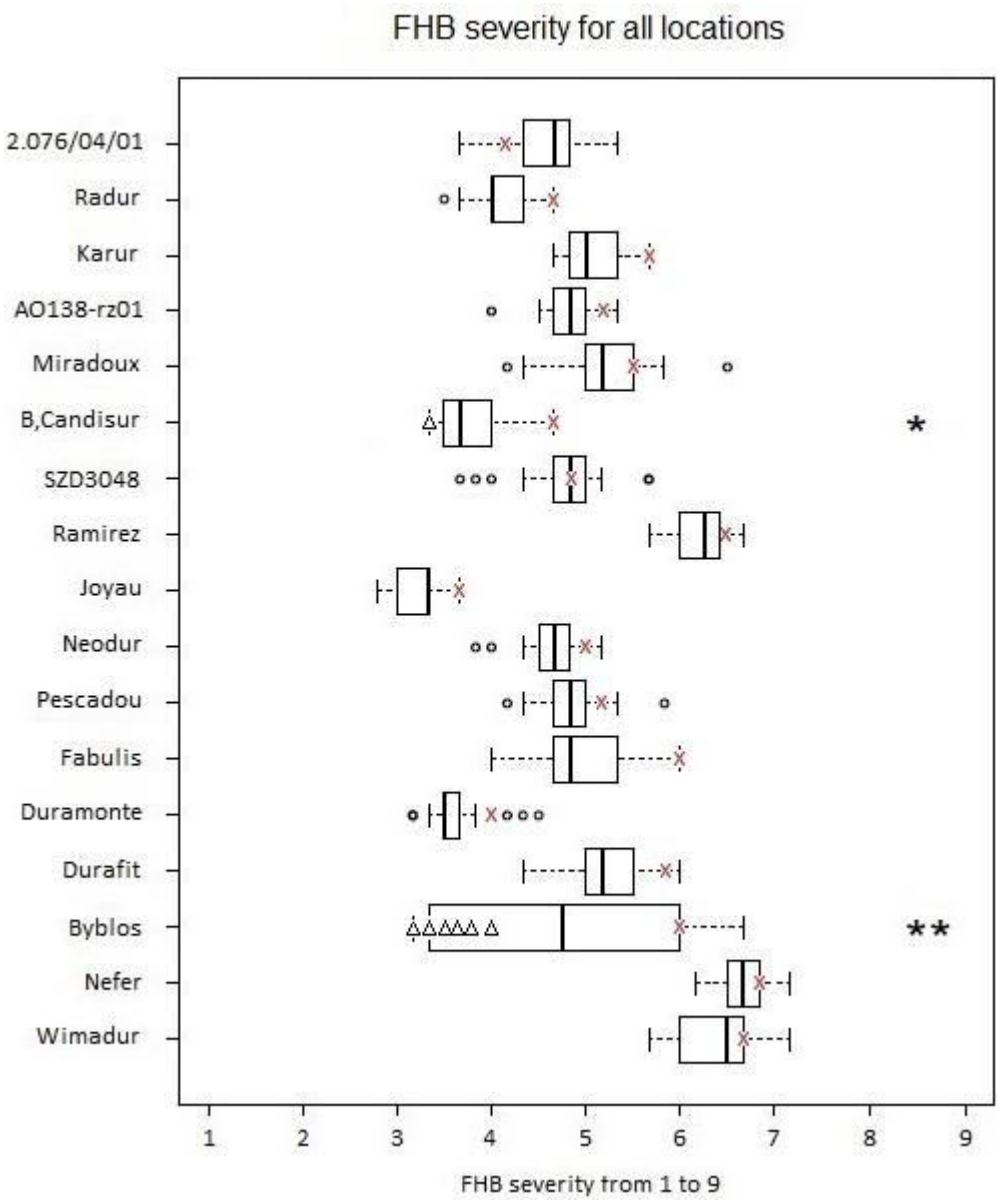


Figure 14: *Boxplot of the 17 durum varieties and their PSVs each for FHB severity means (measured on a 1 to 9 scale) from all locations. The red crosses display the initial varieties, the triangles show significantly different PSVs and the stars indicate significantly (*) or highly significantly (**) different PSVs.*

Figure 15 shows boxplots for FHB severity for every location separately. As for all locations together, a Wilcoxon rank-sum test was carried out individually for each location. Due to the small number of values - the two repetitions for each PSV and initial variety, no significant difference could be identified between any initial variety and PSVs. The three varieties, Buck Candisur, Fabulis and Byblos stand out because the medians of the PSVs showed higher resistances than the median of the initial varietys in each location. At the location Tulln, there were six instances where the initial varieties showed less or the same susceptibility as the median of the PSVs. Especially the breeding line 2.076/04/01 at which the average of the initial varieties showed the highest resistance with 2.5 compared to the PSVs with a mean of 4.5. At the location Hoh only within the variety Neodur the initial variety reached on average higher FHB resistance (5.5) than the median of the PSVs with 6. At Oli the variety Miradoux was the only one at which the initial variety reached a higher resistance of one scale point with 4.5 compared to the median of the PSVs with 5.5, but in this case the mean of the initial varieties represents an outlier.

Comparing the locations to each other the most conspicuous characteristic of the boxplots is that the varieties which were grown in Tulln showed on average the lowest disease severities, while the varieties of Hoh and Oli were roughly at the same level concerning the FHB severity. What is noteworthy for all locations is the large range of PSVs of Byblos for FHB severity from about 3 to 7 scale points.

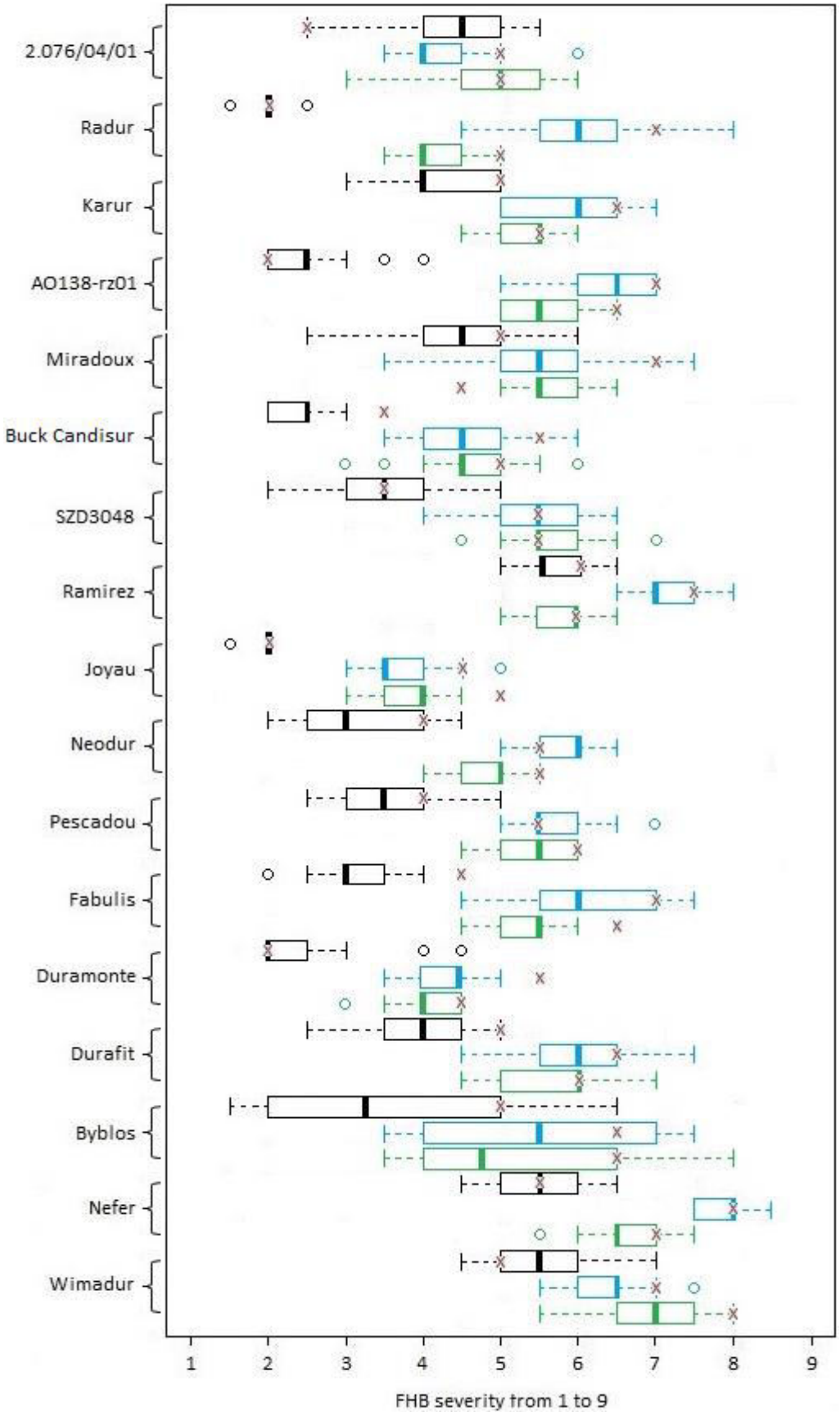


Figure 15: *Boxplot of the 17 durum varieties and their PSVs each for FHB severity means (measured on a 1 to 9 scale) from each location separately. Black boxplots indicate data from Tulln, blue from Hoh and green from Oli. The red crosses display the initial varieties.*

3.8 Comparison of the PSVs with their initial durum variety for PH

In figure 16 the differences of the initial varieties and their PSVs in terms of PH are shown to evaluate the effect of phenotypic selection under FHB disease pressure on this trait. However, this also serves to identify outliers within the 17 durum backgrounds, which may point towards seed contamination. Almost all varieties showed plant heights from about 60 cm to 80 cm. The three varieties - Radur, Joyau and the breeding line AO138-rz01, however, yielded higher plants from 80 cm to a maximum of about 100 cm. Noticeably, most of the initial varieties were shorter in PH than the median of the PSVs. Only within the varieties Ramirez, Joyau and Neodur the initial varieties were on average taller than the median of the PSVs. Furthermore, two significant outliers (E121 and E135) within the variety Buck Candisur, were 95 cm and 97 cm tall, amounting to a difference of 20 cm compared to the median of the other plots with 78 cm. These PSVs did not differ significantly in FHB severity. The PSVs E127 and E141 mentioned in chapter 3.7 at a mean PH of 73 and 74 cm were even shorter than the median of the initial varieties. Another outlier (E145) appeared within the breeding line SZD3048. The second significantly different PSV is E162 within this breeding line. Furthermore, the variety Joyau shows three PSVs (E197, E198 and E211) significantly shorter than the median of the initial variety. Within the variety Byblos, five PSVs (E338, E341, E342, E347 and 350) were significantly shorter than their initial varieties. Each of those PSVs differed also significantly in terms of FHB resistance to their initial variety see chapter 3.7.

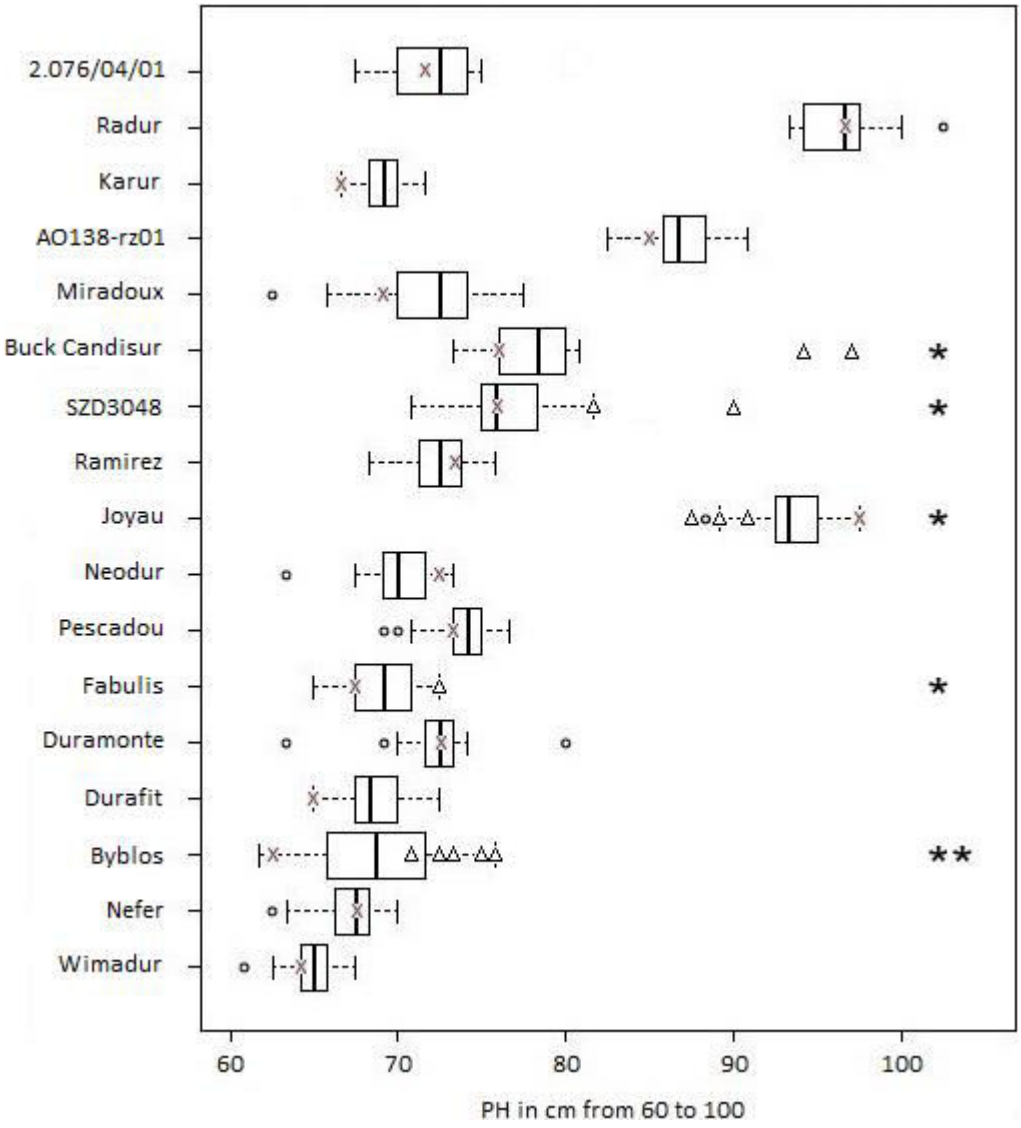


Figure 16: *Boxplot of the 17 durum varieties and their PSVs each for PH means (measured in cm) from all locations. The red crosses display the initial varieties, the triangles show significantly different PSVs and the stars indicate significantly (*) or highly significantly (**) different PSVs.*

3.9 Comparison of the PSVs with their initial durum variety for earliness

When comparing the PSVs with their initial varieties, most of the initial varieties were flowering earlier than their PSVs. Except for the variety Miradoux, within which five PSVs flowered significantly earlier than the initial varieties. All initial varieties were earlier or as early as the mean of their PSVs. For the trait *earliness* there were eleven varieties within which significantly different PSVs to their initial varieties were detected. Within the variety Buck Candisur there is one PSV significantly different to the initial varieties (E135). It is also significantly different in terms of PH but not in terms of FHB resistance. For the variety Byblos, there are six cases of significantly differing PSV, see Table 8. All those PSVs are also differing significantly either in terms of PH or in FHB severity. Three cases (E338, E347 and E350) are even differing significantly in all the three traits. All other PSVs within the other initial varieties (see Table 8) are only differing in the trait earliness, not in other traits like PH or FHB.

Table 8: PSVs for each variety which differ significantly in terms of earliness to their initial variety. The significance is represented by ** for highly significance or * for significance.

2.076/04/01	Radur	Miradoux	Buck Candisur	SZD3048	Neodur	Fabulis	Duramonte	Durafit	Byblos	Nefer
E003 / *	E025 / *	E104 / *	E135 / **	E147 / *	E232 / *	E283 / *	E292 / *	E319 / *	E337 / *	E360 / *
E006 / *	E031 / *	E107 / *		E153 / *		E286 / *	E308 / *		E338 / *	E365 / *
E012 / *	E035 / *	E113 / *		E154 / **		E287 / *			E347 / *	E374 / *
E013 / *	E038 / *	E117 / *		E155 / *					E350 / **	E378 / *
E022 / *	E045 / *	E120 / *		E156 / *					E351 / *	E379 / *
	E046 / *			E157 / *					E356 / *	
				E158 / **						
				E159 / *						
				E165 / *						
				E167 / *						

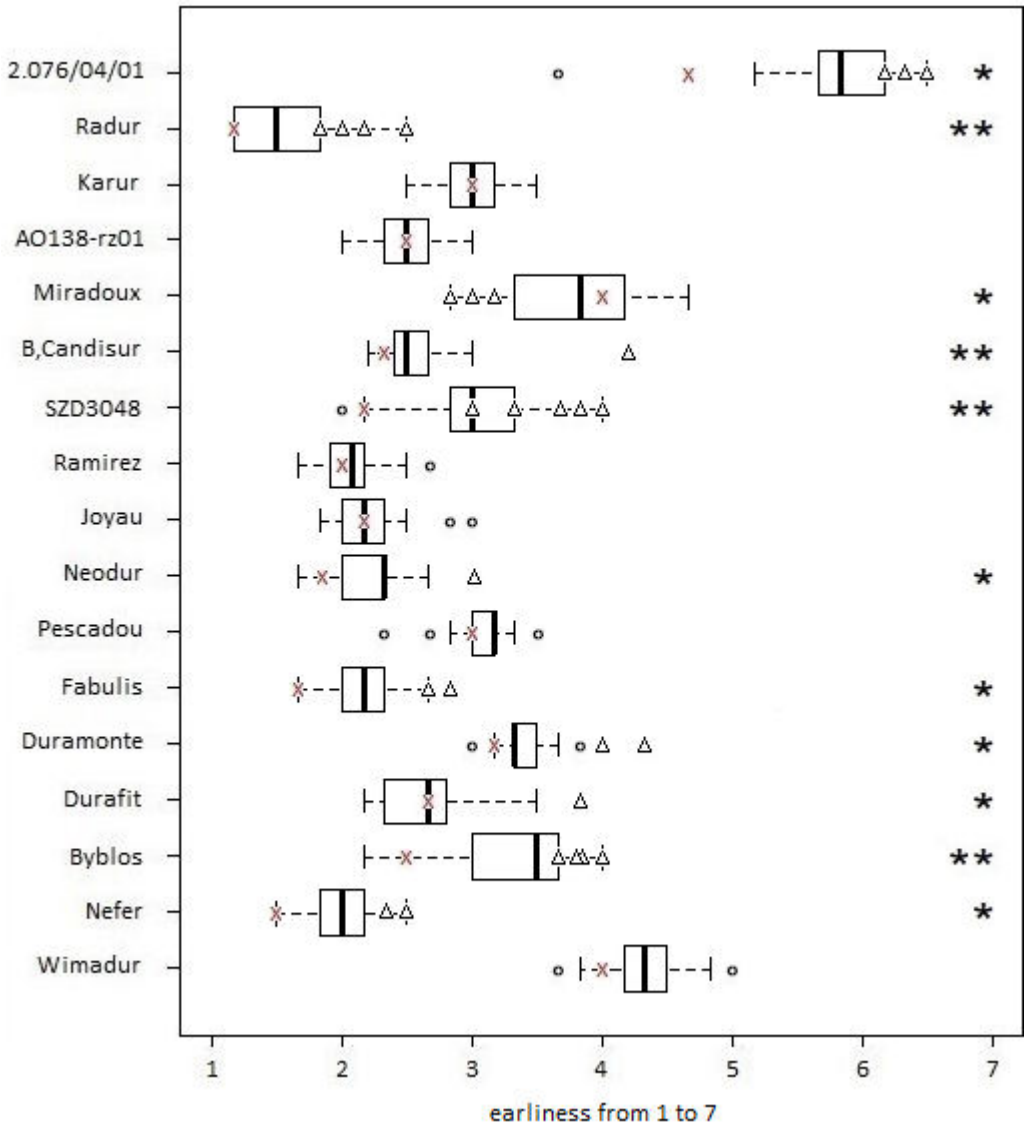


Figure 17: *Boxplot of the 17 durum wheat varieties and their PSVs each for earliness means (from 1 to 7) from all locations. The red crosses display the initial varieties, the triangles show significantly different PSVs and the stars indicate significantly (*) or highly significantly (**) different PSVs.*

3.10 Trait correlations using BLUEs for all locations

In Table 9 correlations are shown between the traits FHB resistance B3 and AUDPC, the PH and earliness. FHB at B3 and PH are correlated negatively with -0.55, PH with AUDPC is weaker correlated with -0.44 but both meaning that taller varieties tended to less disease symptoms. The value for the correlation between PH and earliness is -0.37. No correlation was observed neither between FHB and earliness nor AUDPC and earliness with 0.02 and 0.03. The relationship between FHB and PH is shown as a scatterplot in Figure 18 and 19.

Table 9: *Correlations between the traits FHB severity at B3, AUDPC, PH, and earliness for BLUEs over all locations PSVs and initial varieties. The significance is represented by ** for highly significance, * for significance or blank for no significance. The number below shows the correlation coefficient.*

	FHB B3	AUDPC	PH
PH	** -0.55	** -0.44	
earliness	0.02	0.03	** -0.37

To show the correlation between the FHB severity and the trait earliness for every location, a table was plotted below. The correlation for Tulln was positive with (r: 0.34) and for Hoh a negative correlation was calculated with (r: -0.39). The correlation for the location Oli was close to zero with (r: -0.02).

Table 10: *Correlations between BLUEs of FHB severity at B3 and earliness for every location separately for PSVs and initial varieties. The significance is represented by ** for highly significance, * for significance or blank for no significance. The number below shows the correlation coefficient.*

	FHB Tulln	HOH	OLI
earliness	** 0.34	** -0.39	-0.02

3.11 Correlations of FHB and PH using means for all locations

In Figure 18 and 19 scatterplots were generated from the means of the initial varieties and PSVs from all locations to visualise the association between FHB susceptibility and PH. The correlations between PH and FHB over all PSVs and initial varieties was -0.55, see Figure 18. Within the varieties Joyau, Buck Candisur, SZD3048, Fabulis and Byblos were PSVs detected (see Table 11) which differed significantly in terms of PH to their initial varieties which can be observed in detail in Figure 19.

Table 11: *PSVs for each variety which differ significantly in terms of PH to their initial variety. The significance is represented by ** for highly significance or * for significance.*

Byblos	Joyau	Buck Candisur	SZD3048	Fabulis
E338 / *	E197 / *	E121 / *	E145 / *	E265 / *
E341 / *	E198 / *	E135 / *	E162 / *	E287 / *
E342 / *	E211 / *			
E347 / *				
E350 / **				

Only within the variety Joyau there were significantly shorter PSV's compared to the initial variety. The two outstanding PSVs within the variety Buck Candisur are on average almost 20 cm taller than the initial variety and regarding the trait FHB susceptibility they show one scale number less severity than the initial lines but the difference in the FHB trait shows no significance (see chapter 3.7). Byblos and their PSVs, is the only background where PSVs with significant differences to the original variety were detected for both traits, PH and FHB severity (see chapter 3.7).

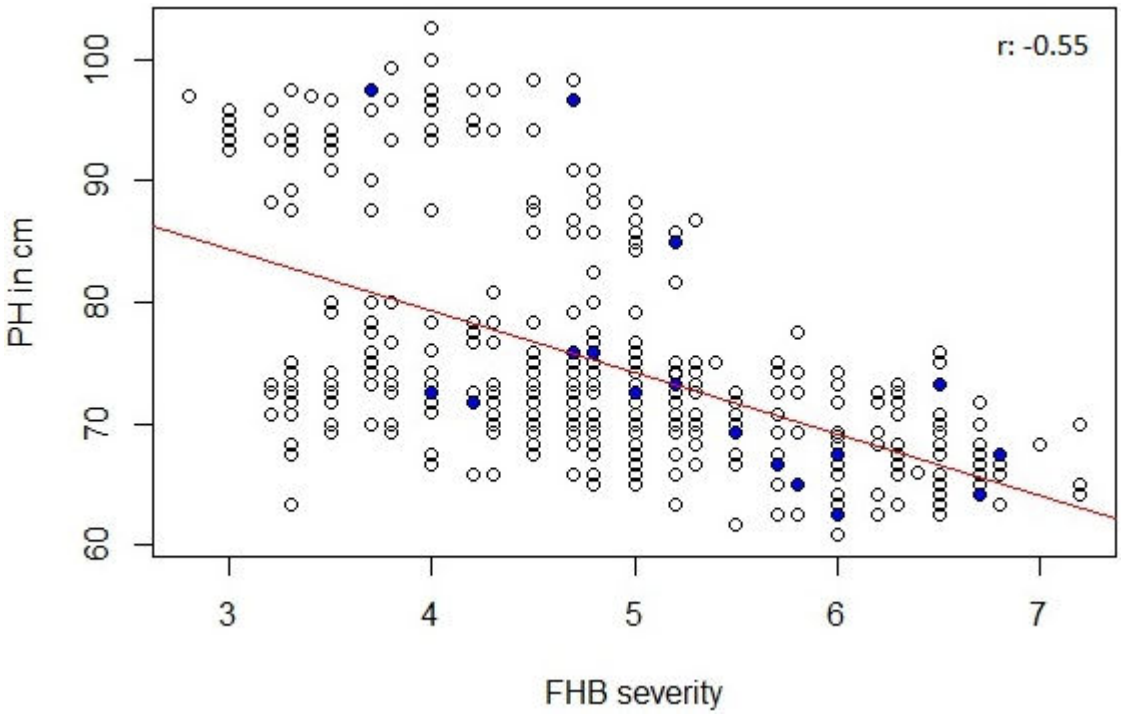


Figure 18: *scatterplot showing the relationship between FHB severity and PH in cm. The blue dots represent the means of the initial varieties and the blank dots represent the PSVs. Top right the correlation coefficient r is shown.*

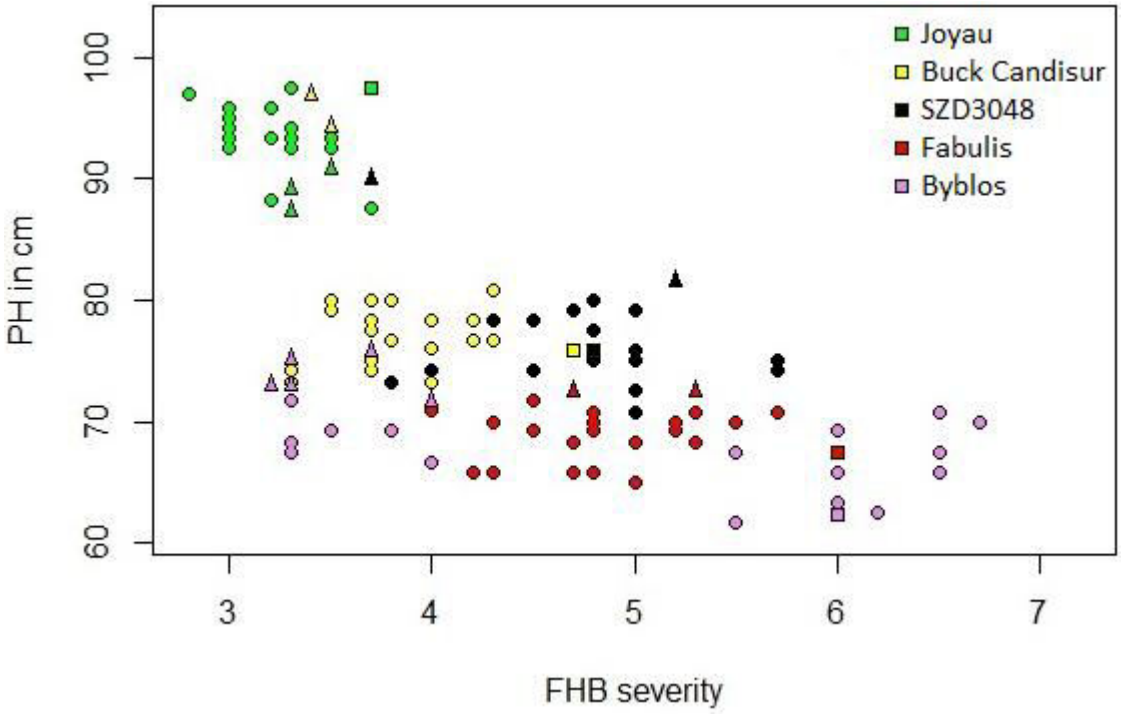


Figure 19: *scatterplot showing the relationship between FHB severity and the PH in cm. The green colour represents variety Joyau, yellow represents Buck Candisur, black represents SZD3048, red represents Fabulis and purple represents Byblos. The coloured squares represent the average of the initial varieties, the triangles stand for the PSVs which were differing significantly from the initial lines in terms of PH.*

4 Discussion

4.1 The influence of infection pressure on FHB susceptibility

The objective of this study was to ascertain if the selection for FHB resistance under repeated infection pressure can lead to lower disease severities compared to the initial homozygous genotype. The underlying concept was to change the expression of pre-existing genes by inducing stress to the plants via a pathogen. Previous studies conducted by Haber et al. (2011) and Comeau et al. (2011) have already demonstrated that this may be a promising avenue of research. In this study. By observing the overall data, it can be seen that the maximum severities reached higher values within the PSVs, which can be explained by the higher number of lines and since some PSVs showed higher susceptibility than the initial varieties. Although a high value of the variance is explained by the genotype effect and a high number of replications was conducted, there were only two backgrounds with significantly more resistant PSVs compared to their initial varieties. Comeau et al. (2011) and Haber et al. (2011) showed that induced stress caused by a treatment with BYDV or WSMV can lead to tolerance against both, FHB and the virus. Kumar et al. (2020) showed that treatment with 5-methyl-azacytidine to remove cytosine DNA methylation in the tested durum lines resulted in up to 30% less FHB susceptibility of durum wheat in comparison with the susceptible controls and the parental lines. This study showed that after repeated FHB inoculation and selection of most resistant wheat heads, a weak effect on the FHB resistance of the progeny could be observed. Furthermore, PSVs within two initial varieties showed significantly less susceptibility to the fungus. Thus, future research should involve genotyping to determine if all PSVs were in fact offspring lines of the initial varieties.

4.2 The relationship of plant height and FHB severity

Many studies have already shown that there is a strong linkage between the FHB susceptibility and the plant height of wheat (e.g.: Buerstmayr, Steiner and Buerstmayr, 2020, Zhu et al., 1999 and Hilton et al., 1999). The relationship can be explained by passive resistance where the distance between the infectiouse material on the ground and the ears is greater in higher plants. Another important factor is microclimate. The humidity at the height level of the ears decreases with increasing canopy height. Also, windspeed increases which contributes to dry the wett plant parts after precipitation. Furthermore, He et al. (2016) and Yan et al. (2011) suggested that Rht genes have considerable influence on FHB resistance. In

this study, the linkage between PH and FHB severity was confirmed. For the initial varieties the correlation coefficient (r: -0.63) was significant. For all lines taken together the linkage was as strong, but still distinct with (r: -0.55). Some PSVs differed significantly from the initial lines in terms of PH. Most noticable were the five cases within the variety Byblos at which even PH and FHB severity differed significantly from initial lines. Whether epigenetic effects were involved in the PH (taller vs. shorter varieties) and whether this influenced FHB tolerance has to be determined in further experiments. Yet, prior to that, it should be ensured that all PSV's are indeed variants of their assumed backgrounds. Johannes et al. (2009) found out that phenotypic alteration of the PH and the flowering time of *Arabidopsis thaliana* can be partly explained by epigenetic effects such as DNA methylation and can be inherited across generations. So it is also conceivable that a changed PH in durum wheat is caused by epigenetics. The highest difference in PH was observed for the variety with a Buck Candisur-background. Buck Candisur was (PH: 75 cm) 20 cm shorter than two of the PSVs (PH: ~95 cm) which constitutes a big difference. Both of the two lines showed lower FHB severities (FHB B3: ~3.5) than Buck Candisur (FHB B3: ~4.7) but differences were not significant. Two other PSVs (E127 and E141) differed significantly in terms of FHB severity, but were shorter than the initial varieties. Within the variety Joyau there were significant differences detected three cases for the PH, but all PSVs were shorter or of the same height as the initial varieties. Despite the trend the PSVs showed lower FHB severity than the initial varieties. Within the breeding line SZD3048 there were two PSVs which differed significantly from their backgrounds but only one showed better results in terms of FHB severity. However, since in this study only two varieties showed significant differences in susceptibility to FHB and an overlay with significantly taller plants was observed, the origin of such changes in the PSVs remains undetermined.

4.3 Environmental effect and Flowering date in association with FHB severity

Varieties grown in Tulln showed weaker disease progression in comparison to the other locations. This phenomenon can be explained by the temperatures during the flowering period. Mastretta and Rossi (2016), and Tschanz and Horst (1976) showed that higher temperatures promote the infection process of *Fusarium spp.* Macroconidia production and mycelial growth of *F. culmorum* increases with increasing temperature till about 29 °C (Tschanz and Horst, 1976). The average temperatures in Tulln and Hoh were about 20 °C in June, while in Oli the mean was about 17 °C (see Figures 1a to 1c). The temperature in Tulln

was strongly increasing after May to June from 10 to 20 °C on average, the increase of temperature in Hoh and Oli was not that strong with 15 to 19 °C in Hoh and 13 to 17 °C in Oli on average. This could explain the positive correlation coefficient in Tulln and the negative correlation in Hoh between FHB severity and earliness. In Tulln the late flowering plants met high temperatures whereas in Hoh the temperatures for the early flowering plants were comparably high. Also, the minimum temperatures during the nights decreased in Hoh and Oli more than in Tulln. The low correlation coefficient of 0.01 between FHB severity and the trait earliness for all locations derives from the rescinding effect of positive and negative correlations. High correlations were not expected since spray inoculation mimics the natural infection process, however, not to the extent of e.g. grain spawn inoculation (Buerstmayr, Ban and Anderson, 2009). In Tulln and Hoh the correlation coefficient was very similar with (r: 0.34) for Tulln and (r: -39) in Hoh but with opposite direction. In Oli the correlation between earliness and FHB was close to zero. Since the temperatures at this location were not increasing as much, there is an indication that the flowering timing played a less important role for the infection process. In some studies, an association between flowering date and FHB severity cannot be confirmed (Buerstmayr and Buerstmayr, 2015).

In this study eleven initial varieties with in total 45 PSVs were detected to differ significantly in terms of earliness to their initial varieties. Also, for this trait there remains some uncertainty whether the PSVs were in fact real variants of their respective backgrounds. Especially within the variety Byblos the three PSVs (E338, E347 and E350) which differed significantly in all three traits. Also one PSV from the Buck Candisur background showed an overlapping effect with the trait PH. As there is a strong interaction between temperature, humidity and FHB severity hence the association between flowering date and FHB severity is probably not always genetically controlled. Some studies identify a correlation between flowering date and FHB severity. There are 25 % overlapping QTL for flowering date with QTL for FHB (Buerstmayr, Steiner and Buerstmayr, 2020). As in this study also in other publications depending on the weather conditions a positive, a negative or no correlation between FHB severity and flowering date can be detected (Buerstmayr et al., 2008).

Gilsinger et al. (2005) showed in their study that the short time span and varieties which flower more briefly and with heads flowering more narrowly have a lower risk to get infected by *Fusarium spp*. Manstretta and Rossi (2015) pointed out that the weather conditions during flowering period, especially temperature and humidity play a siginificant role for mycelial groth and infection process. This is in concordance with what was found in the present study, which found no correlation for the trait earliness and FHB severity throughout all locations. For the location Tulln only a weak positive correlation was found and for Hoh a negative

correlation was calculated. Due to the negative and positive correlations in Tulln and Hoh the correlation over all locations were abrogated.

From these results it can be concluded that the trait earliness per se does not play a major role for FHB severity, but the environmental factors like temperature at flowering and plant architecture are significant for the infection process, which supports the results of other studies such as Manstretta and Rossi (2015), Gilsinger et al. (2005), Parry, Jenkinson and McLeod (1995) and Tschanz and Horst (1976).

4.4 Conclusion and outlook

In all analysed traits significantly differing PSVs were detected. Since the low number of significantly different PSVs within the trait FHB severity it can be assumed that the epigenetic effect played a subordinate role for the FHB resistance. The next step should be a genotyping to check if in fact all PSVs are variants of their initial varieties, further investigations can be afterwards carried out to ascertain whether the morphological and physiological changes underlie an epigenetic alteration of certain genes. Also, the current study cannot exclude that potential seed-contamination may have played a role in the findings like increased FHB resistance, taller plants, or later flowering plants, presented in this thesis. In particular, for the varieties Buck Candisur and Byblos, the overlapping in significance of two to three traits may be an indicator of seed-contamination.

Finally, it may be worthwile to study a larger number of generations under infection pressure or systamic stress evoked by a pathogen and abiotic stress to improve resistance to FHB.

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Appendix

Table 12: *means of initial varieties (mean i.v.), means of PSVs (mean PSVs) and P-values (P-v.) of a Wilcoxon rank-sum-test between initial and PSVs for FHB at B3. The results are ordered ascendingly by E-numbers.*

2.076/04/01			Radur			Karur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
4.17	4.5	1.000	4.67	4.00	0.560	5.67	5.17	0.282
4.17	4.5	1.000	4.67	3.83	0.566	5.67	4.67	0.197
4.17	4.5	1.000	4.67	4.17	0.807	5.67	5.17	0.498
4.17	4.67	0.492	4.67	4.00	0.562	5.67	4.67	0.121
4.17	5.2	0.131	4.67	4.00	0.560	5.67	5.67	0.933
4.17	4.83	0.591	4.67	4.33	0.934	5.67	5.00	0.177
4.17	4.67	0.775	4.67	4.00	0.560	5.67	4.83	0.271
4.17	4.67	0.775	4.67	4.33	0.803	5.67	5.50	0.868
4.17	4.67	0.796	4.67	3.83	0.458	5.67	5.00	0.402
4.17	5.17	0.180	4.67	3.83	0.566	5.67	4.83	0.198
4.17	4.17	0.730	4.67	4.17	0.680	5.67	4.83	0.177
4.17	4.83	0.340	4.67	4.00	0.568	5.67	5.17	0.678
4.17	4.00	0.666	4.67	4.00	0.560	5.67	5.00	0.177
4.17	3.83	0.547	4.67	4.67	0.934	5.67	5.50	0.718
4.17	4.83	0.531	4.67	4.17	0.672	5.67	4.80	0.071
4.17	3.67	0.356	4.67	4.00	0.686	5.67	4.83	0.401
4.17	3.67	0.356	4.67	4.33	0.804	5.67	5.17	0.498
4.17	4.33	0.794	4.67	4.50	0.934	5.67	4.67	0.121
4.17	5.33	0.181	4.67	3.83	0.458	5.67	5.33	0.546
4.17	4.83	0.531	4.67	4.50	0.935	5.67	5.00	0.073
4.17	4.67	0.796	4.67	3.67	0.459	5.67	5.50	0.739
4.17	4.67	0.591	4.67	3.50	0.281	5.67	4.83	0.284
4.17	4.83	0.531	4.67	4.17	0.680	5.67	5.33	0.389
4.17	4.67	0.864	4.67	4.00	0.562	5.67	5.00	0.383

AO138-rz01			Miradoux			B. Candisur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
5.17	5.17	1.000	5.50	5.17	0.933	4.67	3.50	0.114
5.17	4.83	0.807	5.50	6.50	0.183	4.67	3.83	0.155
5.17	4.50	0.446	5.50	5.50	0.928	4.67	4.17	0.491
5.17	4.67	0.618	5.50	5.67	0.672	4.67	3.50	0.114
5.17	5.00	1.000	5.50	4.33	0.241	4.67	4.33	0.869
5.17	4.83	0.742	5.50	5.17	0.797	4.67	3.67	0.209
5.17	4.67	0.680	5.50	5.50	1.000	4.67	3.33	0.047
5.17	5.00	0.867	5.50	4.83	0.557	4.67	4.33	1.000
5.17	4.83	0.745	5.50	5.17	0.673	4.67	3.50	0.114
5.17	4.50	0.510	5.50	5.50	1.000	4.67	3.50	0.156
5.17	4.83	0.807	5.50	4.67	0.345	4.67	3.67	0.209
5.17	4.67	0.558	5.50	5.17	0.673	4.67	4.00	0.410
5.17	4.83	0.739	5.50	5.17	0.797	4.67	3.67	0.134
5.17	5.33	1.000	5.50	5.40	1.000	4.67	4.33	0.677
5.17	5.00	0.678	5.50	5.17	0.797	4.67	3.40	0.193
5.17	4.67	0.742	5.50	4.83	0.389	4.67	4.17	0.616
5.17	4.67	0.625	5.50	4.17	0.192	4.67	4.00	0.273
5.17	5.17	1.000	5.50	5.33	1.000	4.67	3.67	0.134
5.17	4.83	0.742	5.50	5.33	1.000	4.67	3.67	0.209
5.17	4.50	0.510	5.50	5.00	0.507	4.67	3.83	0.391
5.17	5.00	0.933	5.50	5.00	0.653	4.67	3.33	0.047
5.17	4.00	0.212	5.50	5.83	0.555	4.67	3.83	0.241
5.17	5.00	0.933	5.50	5.17	0.863	4.67	3.67	0.209
5.17	4.50	0.618	5.50	4.67	0.622	4.67	4.00	0.639

SZD 3048			Ramirez			Joyau		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
4.83	3.67	0.285	6.50	6.00	0.452	3.67	3.00	0.359
4.83	5.00	1.000	6.50	6.50	1.000	3.67	3.33	0.541
4.83	4.50	0.743	6.50	6.33	0.801	3.67	3.33	0.541
4.83	4.83	1.000	6.50	6.00	0.401	3.67	3.17	0.562
4.83	5.67	0.323	6.50	6.00	0.452	3.67	3.33	0.541
4.83	4.67	1.000	6.50	6.33	0.865	3.67	3.33	0.541
4.83	5.00	0.935	6.50	6.00	0.452	3.67	3.50	0.803
4.83	4.83	1.000	6.50	6.67	0.868	3.67	3.33	0.541
4.83	4.33	0.684	6.50	6.00	0.456	3.67	3.33	0.676
4.83	4.50	0.805	6.50	6.33	0.720	3.67	3.67	0.932
4.83	5.00	0.804	6.50	5.83	0.316	3.67	3.00	0.359
4.83	4.83	1.000	6.50	6.50	1.000	3.67	3.50	0.798
4.83	3.83	0.324	6.50	6.00	0.564	3.67	3.00	0.359
4.83	4.00	0.413	6.50	5.67	0.203	3.67	3.50	0.798
4.83	5.00	0.737	6.50	6.33	0.720	3.67	2.80	0.298
4.83	4.83	1.000	6.50	6.00	0.388	3.67	3.00	0.359
4.83	4.83	0.934	6.50	6.17	0.673	3.67	3.17	0.445
4.83	5.17	0.744	6.50	6.50	1.000	3.67	3.00	0.359
4.83	5.00	0.737	6.50	6.50	1.000	3.67	3.33	0.676
4.83	5.00	0.869	6.50	6.17	0.619	3.67	3.33	0.541
4.83	5.00	0.935	6.50	6.33	0.720	3.67	3.17	0.445
4.83	5.00	0.870	6.50	6.17	0.619	3.67	3.00	0.341
4.83	5.67	0.284	6.50	6.33	0.794	3.67	3.00	0.359
4.83	4.83	1.000				3.67	3.33	0.676

Neodur			Pescadou			Fabulis		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
5.00	4.50	0.735	5.17	4.83	0.742	6.00	5.50	0.731
5.00	4.50	0.616	5.17	5.33	0.865	6.00	4.67	0.157
5.00	4.67	0.406	5.17	5.00	0.869	6.00	4.00	0.093
5.00	4.50	0.487	5.17	5.17	1.000	6.00	4.83	0.216
5.00	4.83	0.445	5.17	4.67	0.510	6.00	4.83	0.186
5.00	4.67	0.798	5.17	5.33	0.557	6.00	4.33	0.060
5.00	4.67	0.324	5.17	4.83	0.869	6.00	4.67	0.284
5.00	4.33	0.560	5.17	4.67	0.452	6.00	4.83	0.216
5.00	4.50	0.735	5.17	5.33	0.802	6.00	5.67	0.675
5.00	4.83	0.865	5.17	4.33	0.246	6.00	4.83	0.131
5.00	4.50	0.487	5.17	5.00	0.859	6.00	5.17	0.565
5.00	5.00	0.932	5.17	4.67	0.673	6.00	5.33	0.623
5.00	5.17	0.869	5.17	4.50	0.273	6.00	4.50	0.065
5.00	4.83	0.605	5.17	4.67	0.797	6.00	5.00	0.459
5.00	5.17	0.729	5.17	5.00	1.000	6.00	5.00	0.453
5.00	4.33	0.437	5.17	4.83	0.869	6.00	5.33	0.408
5.00	4.00	0.216	5.17	4.83	0.727	6.00	4.67	0.183
5.00	3.83	0.123	5.17	5.00	0.865	6.00	5.17	0.247
5.00	4.50	0.487	5.17	4.83	0.673	6.00	4.33	0.084
5.00	4.83	0.865	5.17	4.50	0.359	6.00	4.17	0.061
5.00	4.83	0.557	5.17	5.83	0.300	6.00	5.17	0.323
5.00	4.33	0.672	5.17	4.67	0.452	6.00	5.50	0.742
5.00	4.67	0.504	5.17	5.00	0.859	6.00	4.50	0.120
5.00	4.67	0.798	5.17	4.17	0.209	6.00	5.33	0.362

Duramonte			Durafit			Byblos		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
4.00	3.33	0.410	5.83	5.50	0.675	6.00	6.50	0.357
4.00	3.50	0.503	5.83	5.00	0.295	6.00	3.83	0.011
4.00	3.67	0.676	5.83	5.00	0.295	6.00	3.67	0.007
4.00	3.50	0.451	5.83	5.00	0.340	6.00	5.50	0.445
4.00	4.50	0.675	5.83	4.83	0.391	6.00	4.00	0.042
4.00	3.17	0.354	5.83	6.00	0.915	6.00	3.17	0.004
4.00	3.50	0.618	5.83	5.33	0.591	6.00	4.00	0.011
4.00	3.83	0.868	5.83	5.33	0.591	6.00	6.67	0.190
4.00	3.83	0.933	5.83	5.00	0.459	6.00	6.00	0.933
4.00	4.17	1.000	5.83	5.50	0.864	6.00	6.00	1.000
4.00	3.33	0.351	5.83	4.33	0.104	6.00	3.33	0.011
4.00	3.50	0.618	5.83	5.00	0.295	6.00	3.33	0.007
4.00	3.33	0.351	5.83	5.50	1.000	6.00	6.00	0.933
4.00	3.50	0.503	5.83	5.17	0.493	6.00	3.33	0.011
4.00	3.50	0.503	5.83	5.50	1.000	6.00	3.33	0.007
4.00	3.50	0.621	5.83	4.83	0.558	6.00	3.33	0.004
4.00	3.33	0.457	5.83	5.17	0.340	6.00	6.50	0.562
4.00	3.17	0.318	5.83	5.17	0.438	6.00	6.50	0.683
4.00	3.67	0.620	5.83	5.00	0.438	6.00	6.17	0.933
4.00	3.67	0.559	5.83	5.17	0.531	6.00	5.50	0.932
4.00	4.33	1.000	5.83	5.83	0.730	6.00	3.50	0.004
4.00	3.50	0.503	5.83	5.33	1.000			
4.00	3.50	0.503	5.83	4.67	0.123			
4.00	3.50	0.451	5.83	4.50	0.244			

Nefer			Wimadur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
6.83	6.50	0.619	6.67	6.67	1.000
6.83	6.83	1.000	6.67	6.50	0.865
6.83	7.17	0.611	6.67	6.33	0.680
6.83	7.00	0.933	6.67	6.83	1.000
6.83	6.50	0.677	6.67	6.67	1.000
6.83	6.50	0.619	6.67	6.50	0.738
6.83	6.50	0.619	6.67	5.67	0.249
6.83	6.33	0.562	6.67	6.83	0.865
6.83	6.50	0.740	6.67	5.67	0.273
6.83	6.33	0.562	6.67	6.00	0.456
6.83	6.33	0.456	6.67	6.33	0.558
6.83	6.50	0.740	6.67	5.67	0.236
6.83	6.50	0.740	6.67	6.67	0.934
6.83	6.83	1.000	6.67	5.83	0.403
6.83	7.17	0.611	6.67	6.33	0.802
6.83	6.83	1.000	6.67	6.50	0.868
6.83	6.67	0.801	6.67	6.40	0.849
6.83	6.83	1.000	6.67	6.17	0.507
6.83	6.67	0.868	6.67	6.50	0.868
6.83	6.83	0.933	6.67	6.00	0.456
6.83	6.67	0.933	6.67	6.00	0.456
6.83	6.67	0.801	6.67	7.17	0.605
6.83	6.17	0.458	6.67	6.67	0.934
6.83	6.50	0.740	6.67	6.50	1.000

Table 13: *means of initial varieties (mean i.v.), means of PSVs (mean PSVs) and P-values (P-v.) of a Wilcoxon rank-sum-test between initial and PSVs for PH. The results are ordered ascendingly by E-numbers.*

2.076/04/01			Radur			Karur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
71.7	67.5	0.461	96.7	95.8	0.788	66.7	70.8	0.505
71.7	69.2	0.807	96.7	96.7	1.000	66.7	69.2	0.743
71.7	72.5	0.935	96.7	95.0	0.794	66.7	70.0	0.591
71.7	75.0	0.684	96.7	94.2	0.933	66.7	69.2	0.741
71.7	74.0	0.707	96.7	93.3	0.273	66.7	67.5	1.000
71.7	75.0	0.512	96.7	94.2	0.423	66.7	69.2	0.452
71.7	74.2	0.741	96.7	100.0	0.362	66.7	67.5	1.000
71.7	70.0	0.739	96.7	97.5	0.799	66.7	71.7	0.242
71.7	75.0	0.568	96.7	93.3	0.337	66.7	66.7	0.802
71.7	74.2	0.615	96.7	99.2	0.461	66.7	68.3	0.565
71.7	72.5	1.000	96.7	94.2	0.666	66.7	67.5	1.000
71.7	70.0	0.807	96.7	102.5	0.103	66.7	70.8	0.360
71.7	73.3	0.742	96.7	93.3	0.802	66.7	69.2	0.546
71.7	70.0	0.935	96.7	98.3	0.548	66.7	67.5	1.000
71.7	72.5	0.935	96.7	97.5	0.923	66.7	70.0	0.618
71.7	70.0	1.000	96.7	97.5	0.784	66.7	70.8	0.360
71.7	70.0	0.935	96.7	97.5	0.931	66.7	70.0	0.408
71.7	70.8	0.870	96.7	98.3	0.675	66.7	69.2	0.615
71.7	75.0	0.563	96.7	96.7	1.000	66.7	69.2	0.615
71.7	70.8	0.802	96.7	94.2	0.546	66.7	70.8	0.360
71.7	74.2	0.548	96.7	95.8	0.198	66.7	69.2	0.797
71.7	71.7	1.000	96.7	96.7	1.000	66.7	69.2	0.615
71.7	73.3	0.737	96.7	95.0	0.931	66.7	70.0	0.437
71.7	70.0	0.676	96.7	96.7	0.931	66.7	69.2	0.797

AO138-rz01			Miradoux			B. Candisur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
85.0	85.0	1.000	69.2	70.8	1.000	75.8	94.2	0.039
85.0	90.8	0.137	69.2	62.5	0.222	75.8	80.0	0.208
85.0	87.5	0.498	69.2	72.5	0.622	75.8	76.7	0.862
85.0	86.7	0.743	69.2	72.5	0.805	75.8	80.0	0.246
85.0	88.3	0.410	69.2	73.3	0.616	75.8	76.7	0.802
85.0	85.8	0.934	69.2	70.0	1.000	75.8	75.0	0.931
85.0	85.8	0.802	69.2	72.5	0.805	75.8	73.3	0.869
85.0	85.0	0.622	69.2	76.7	0.211	75.8	80.8	0.102
85.0	82.5	0.564	69.2	71.7	0.803	75.8	79.2	0.314
85.0	88.3	0.512	69.2	66.7	0.564	75.8	80.0	0.300
85.0	88.3	0.413	69.2	75.8	0.241	75.8	77.5	0.662
85.0	90.8	0.188	69.2	70.8	0.934	75.8	73.3	1.000
85.0	88.3	0.352	69.2	71.7	0.869	75.8	74.2	1.000
85.0	86.7	0.738	69.2	75.0	0.344	75.8	78.3	0.437
85.0	85.8	0.934	69.2	75.0	0.363	75.8	97.0	0.015
85.0	85.8	0.742	69.2	70.0	0.932	75.8	78.3	0.498
85.0	86.7	0.680	69.2	77.5	0.094	75.8	78.3	0.507
85.0	85.8	0.869	69.2	74.2	0.503	75.8	78.3	0.498
85.0	89.2	0.370	69.2	66.7	0.359	75.8	78.3	0.557
85.0	88.3	0.352	69.2	65.8	0.459	75.8	80.0	0.151
85.0	84.2	0.867	69.2	71.7	1.000	75.8	74.2	0.802
85.0	87.5	0.503	69.2	77.5	0.118	75.8	76.7	0.325
85.0	86.7	0.738	69.2	72.5	0.622	75.8	80.0	0.167
85.0	85.8	0.867	69.2	74.2	0.458	75.8	76.0	0.596

SZD 3048			Ramirez			Joyau		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
75.8	90.0	0.016	73.3	74.2	0.862	97.5	92.5	0.150
75.8	75.0	0.445	73.3	75.0	0.432	97.5	92.5	0.052
75.8	78.3	0.473	73.3	73.3	1.000	97.5	93.3	0.073
75.8	75.8	0.924	73.3	71.7	0.677	97.5	88.3	0.062
75.8	75.0	0.673	73.3	73.3	0.932	97.5	93.3	0.402
75.8	79.2	0.227	73.3	73.3	0.932	97.5	87.5	0.026
75.8	79.2	0.100	73.3	73.3	1.000	97.5	90.8	0.030
75.8	80.0	0.214	73.3	71.7	0.546	97.5	94.2	0.402
75.8	78.3	0.112	73.3	74.2	0.862	97.5	97.5	0.928
75.8	74.2	0.673	73.3	72.5	0.718	97.5	87.5	0.198
75.8	75.8	0.930	73.3	72.5	0.865	97.5	95.0	0.226
75.8	75.0	0.673	73.3	75.8	0.498	97.5	93.3	0.073
75.8	73.3	0.490	73.3	68.3	0.402	97.5	95.0	0.316
75.8	74.2	1.000	73.3	69.2	0.177	97.5	92.5	0.052
75.8	70.8	0.056	73.3	68.3	0.498	97.5	97.0	0.623
75.8	77.5	0.527	73.3	74.2	0.862	97.5	94.2	0.242
75.8	77.5	0.849	73.3	69.2	0.271	97.5	93.3	0.073
75.8	81.7	0.029	73.3	70.0	0.383	97.5	95.8	0.612
75.8	72.5	0.390	73.3	75.0	0.432	97.5	94.2	0.280
75.8	75.0	0.931	73.3	71.7	0.523	97.5	89.2	0.018
75.8	75.8	0.863	73.3	70.8	0.401	97.5	95.8	0.432
75.8	79.2	0.100	73.3	72.5	1.000	97.5	93.3	0.150
75.8	74.2	0.787	73.3	71.7	1.000	97.5	92.5	0.215
75.8	77.5	0.528	73.3	74.2	0.862	97.5	94.2	0.280

Neodur			Pescadou			Fabulis		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
72.5	68.3	0.183	73.3	74.2	0.673	67.5	67.5	1.000
72.5	70.8	0.397	73.3	75.0	0.673	67.5	72.5	0.038
72.5	68.3	0.315	73.3	74.2	0.933	67.5	71.0	0.168
72.5	71.7	0.801	73.3	70.0	0.737	67.5	69.2	0.662
72.5	70.8	0.560	73.3	74.2	0.676	67.5	70.8	0.137
72.5	70.0	0.677	73.3	74.2	0.801	67.5	70.0	0.071
72.5	70.0	0.357	73.3	73.3	0.934	67.5	65.8	0.498
72.5	69.2	0.212	73.3	70.8	0.616	67.5	70.0	0.201
72.5	70.8	0.738	73.3	73.3	0.739	67.5	70.8	0.054
72.5	70.8	0.257	73.3	73.3	0.742	67.5	65.8	0.476
72.5	70.0	0.677	73.3	73.3	0.867	67.5	70.0	0.341
72.5	73.3	1.000	73.3	73.3	0.867	67.5	68.3	0.859
72.5	63.3	0.115	73.3	75.0	0.738	67.5	71.7	0.138
72.5	69.2	0.315	73.3	71.7	0.869	67.5	65.0	0.869
72.5	67.5	0.098	73.3	75.0	0.560	67.5	68.3	1.000
72.5	72.5	1.000	73.3	74.2	0.931	67.5	70.8	0.201
72.5	67.5	1.000	73.3	75.8	0.358	67.5	68.3	0.322
72.5	70.0	0.492	73.3	74.2	0.801	67.5	69.2	0.859
72.5	70.0	0.126	73.3	69.2	0.616	67.5	65.8	0.863
72.5	72.5	0.867	73.3	75.8	0.356	67.5	65.8	0.675
72.5	70.0	0.357	73.3	74.2	0.801	67.5	69.2	0.476
72.5	72.5	0.663	73.3	75.0	0.673	67.5	70.0	0.476
72.5	71.7	0.802	73.3	76.7	0.513	67.5	69.2	0.228
72.5	68.3	0.391	73.3	71.7	0.680	67.5	72.5	0.038

Duramonte			Durafit			Byblos		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
72.5	73.3	0.663	65.0	70.8	0.210	62.5	67.5	0.160
72.5	74.2	0.498	65.0	67.5	0.934	62.5	69.2	0.317
72.5	80.0	0.054	65.0	69.2	0.560	62.5	75.8	0.026
72.5	73.3	0.663	65.0	65.8	0.863	62.5	67.5	0.160
72.5	73.3	0.675	65.0	65.0	1.000	62.5	66.7	0.406
72.5	70.8	1.000	65.0	69.0	0.639	62.5	73.3	0.026
72.5	69.2	0.342	65.0	69.2	0.458	62.5	71.7	0.017
72.5	72.5	1.000	65.0	69.2	0.625	62.5	70.0	0.071
72.5	74.2	0.360	65.0	68.3	0.667	62.5	65.8	0.273
72.5	72.5	1.000	65.0	67.5	0.871	62.5	63.3	0.931
72.5	70.8	0.322	65.0	72.5	0.256	62.5	68.3	0.369
72.5	72.5	0.865	65.0	67.5	0.797	62.5	73.3	0.039
72.5	72.5	1.000	65.0	71.7	0.211	62.5	69.2	0.162
72.5	71.7	0.673	65.0	65.8	0.867	62.5	67.5	0.249
72.5	72.5	0.675	65.0	70.8	0.324	62.5	75.0	0.007
72.5	71.7	0.675	65.0	68.3	0.616	62.5	71.7	0.104
72.5	63.3	0.498	65.0	67.5	0.866	62.5	70.8	0.073
72.5	72.5	0.498	65.0	67.5	0.867	62.5	65.8	0.406
72.5	73.3	0.640	65.0	70.0	0.315	62.5	62.5	1.000
72.5	74.2	0.662	65.0	67.5	0.624	62.5	61.7	0.933
72.5	71.7	1.000	65.0	69.2	0.569	62.5	69.2	0.249
72.5	73.3	0.859	65.0	70.0	0.459			
72.5	72.5	1.000	65.0	68.3	0.802			
72.5	70.0	0.866	65.0	70.8	0.411			

Nefer			Wimadur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
67.5	70.0	0.869	64.2	64.2	1.000
67.5	66.7	0.640	64.2	66.7	0.622
67.5	70.0	0.071	64.2	65.8	0.678
67.5	68.3	0.663	64.2	67.5	0.458
67.5	68.3	0.640	64.2	67.5	0.459
67.5	69.2	0.282	64.2	64.2	0.934
67.5	67.5	1.000	64.2	65.0	0.807
67.5	67.5	1.000	64.2	63.3	0.934
67.5	63.3	0.476	64.2	65.0	0.807
67.5	68.3	0.663	64.2	60.8	0.568
67.5	65.8	0.476	64.2	65.8	0.680
67.5	69.2	0.662	64.2	62.5	0.869
67.5	65.8	0.476	64.2	65.0	0.934
67.5	67.5	1.000	64.2	62.5	0.869
67.5	65.0	0.663	64.2	63.3	0.934
67.5	67.5	0.855	64.2	65.0	0.737
67.5	67.5	0.855	64.2	66.0	0.639
67.5	66.7	0.640	64.2	64.2	1.000
67.5	66.7	0.859	64.2	65.8	0.680
67.5	65.8	0.662	64.2	66.7	0.623
67.5	68.3	0.640	64.2	64.2	0.935
67.5	67.5	0.855	64.2	64.2	1.000
67.5	68.3	0.663	64.2	66.7	0.563
67.5	62.5	0.476	64.2	64.2	0.807

Table 14: *means of initial varieties (mean i.v.), means of PSVs (mean PSVs) and P-values (P-v.) of a Wilcoxon rank-sum-test between initial and PSVs for earliness. The results are ordered ascendingly by E-numbers.*

2.076/04/01			Radur			Karur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
4.67	6.00	0.084	1.17	2.50	0.025	3.00	2.83	0.718
4.67	5.83	0.138	1.17	1.17	1.000	3.00	3.17	0.673
4.67	6.17	0.045	1.17	1.33	0.595	3.00	3.00	1.000
4.67	5.83	0.164	1.17	1.17	1.000	3.00	3.00	1.000
4.67	5.60	0.304	1.17	1.17	1.000	3.00	2.67	0.387
4.67	6.33	0.032	1.17	1.33	0.595	3.00	3.00	1.000
4.67	5.67	0.183	1.17	2.00	0.007	3.00	2.83	0.718
4.67	5.33	0.354	1.17	1.67	0.112	3.00	2.50	0.201
4.67	6.00	0.084	1.17	1.67	0.248	3.00	3.00	0.787
4.67	5.17	0.503	1.17	1.17	1.000	3.00	2.83	0.718
4.67	5.33	0.458	1.17	1.83	0.034	3.00	3.00	1.000
4.67	6.50	0.021	1.17	1.67	0.112	3.00	3.17	0.718
4.67	6.17	0.045	1.17	1.83	0.248	3.00	3.50	0.388
4.67	6.17	0.059	1.17	1.83	0.034	3.00	3.00	1.000
4.67	6.17	0.059	1.17	1.17	1.000	3.00	3.00	1.000
4.67	6.00	0.119	1.17	1.17	1.000	3.00	2.83	0.718
4.67	6.00	0.101	1.17	1.50	0.282	3.00	2.83	0.673
4.67	5.67	0.219	1.17	1.50	0.282	3.00	3.00	1.000
4.67	3.67	0.157	1.17	1.33	0.595	3.00	3.17	0.673
4.67	5.83	0.138	1.17	1.67	0.112	3.00	3.33	0.432
4.67	5.83	0.138	1.17	2.17	0.033	3.00	3.33	0.387
4.67	6.33	0.039	1.17	2.17	0.029	3.00	3.00	1.000
4.67	5.83	0.111	1.17	1.17	1.000	3.00	3.00	1.000
4.67	5.67	0.219	1.17	1.33	0.595	3.00	3.33	0.387

AO138-rz01			Miradoux			B. Candisur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
2.50	2.17	0.476	4.00	4.00	1.000	2.33	3.00	0.247
2.50	2.17	0.322	4.00	4.33	0.387	2.33	2.50	0.640
2.50	2.83	0.282	4.00	3.67	0.673	2.33	2.50	0.923
2.50	2.67	0.640	4.00	4.50	0.226	2.33	2.33	0.752
2.50	2.83	0.282	4.00	3.33	0.091	2.33	3.00	0.091
2.50	2.67	0.640	4.00	4.17	0.720	2.33	2.67	0.774
2.50	3.00	0.201	4.00	3.17	0.081	2.33	2.33	0.928
2.50	2.83	0.476	4.00	3.00	0.031	2.33	2.50	0.640
2.50	2.67	0.640	4.00	3.50	0.201	2.33	2.33	0.928
2.50	2.33	0.640	4.00	4.67	0.344	2.33	2.50	0.923
2.50	2.83	0.476	4.00	2.83	0.027	2.33	2.83	0.247
2.50	2.67	0.640	4.00	3.33	0.091	2.33	2.67	0.923
2.50	2.50	1.000	4.00	4.50	0.201	2.33	2.67	0.774
2.50	2.67	0.663	4.00	3.60	0.562	2.33	3.00	0.190
2.50	2.50	0.855	4.00	3.67	0.654	2.33	4.20	0.005
2.50	2.50	1.000	4.00	3.83	1.000	2.33	2.67	0.523
2.50	2.17	0.282	4.00	3.00	0.031	2.33	2.50	0.640
2.50	2.33	0.640	4.00	3.83	0.733	2.33	2.67	0.311
2.50	2.17	0.476	4.00	4.33	0.432	2.33	2.50	0.640
2.50	2.33	0.859	4.00	4.33	0.432	2.33	2.33	0.929
2.50	2.33	0.640	4.00	3.17	0.033	2.33	2.20	0.724
2.50	2.50	0.855	4.00	4.00	1.000	2.33	2.50	0.794
2.50	2.50	1.000	4.00	4.00	1.000	2.33	2.67	0.437
2.50	2.00	0.341	4.00	3.00	0.031	2.33	2.40	0.596

SZD 3048			Ramirez			Joyau		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
2.17	3.17	0.062	2.00	2.17	0.718	2.17	2.17	0.933
2.17	2.83	0.100	2.00	1.67	0.387	2.17	2.00	0.933
2.17	3.33	0.020	2.00	1.83	0.673	2.17	2.17	0.933
2.17	3.17	0.062	2.00	2.33	0.387	2.17	2.17	0.933
2.17	3.17	0.062	2.00	1.83	0.673	2.17	2.33	0.738
2.17	2.00	0.718	2.00	2.00	1.000	2.17	3.00	0.281
2.17	2.33	0.784	2.00	2.33	0.387	2.17	2.33	0.738
2.17	2.17	1.000	2.00	2.17	0.718	2.17	2.17	0.933
2.17	3.33	0.020	2.00	2.00	1.000	2.17	2.83	0.279
2.17	3.67	0.010	2.00	2.17	0.718	2.17	2.50	0.619
2.17	3.00	0.027	2.00	2.17	0.673	2.17	2.17	0.933
2.17	3.00	0.027	2.00	2.00	1.000	2.17	2.33	0.868
2.17	3.33	0.020	2.00	2.67	0.177	2.17	2.00	0.933
2.17	3.67	0.010	2.00	2.50	0.340	2.17	2.00	0.933
2.17	4.00	0.011	2.00	2.00	1.000	2.17	2.20	0.924
2.17	2.83	0.100	2.00	1.83	0.718	2.17	1.83	0.735
2.17	3.00	0.081	2.00	2.33	0.599	2.17	2.00	0.933
2.17	2.50	0.476	2.00	2.17	0.673	2.17	2.00	0.933
2.17	3.00	0.150	2.00	2.00	1.000	2.17	2.33	0.738
2.17	2.83	0.195	2.00	1.67	0.387	2.17	2.00	0.933
2.17	3.33	0.020	2.00	1.83	0.673	2.17	2.00	0.933
2.17	3.00	0.081	2.00	2.17	0.718	2.17	2.33	0.666
2.17	3.83	0.010	2.00	2.17	0.673	2.17	2.00	0.933
2.17	3.00	0.081				2.17	2.33	0.666

Neodur			Pescadou			Fabulis		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
1.83	2.17	0.218	3.00	2.83	0.718	1.67	2.00	0.387
1.83	1.67	0.595	3.00	3.17	0.718	1.67	1.83	0.784
1.83	2.33	0.218	3.00	2.83	0.733	1.67	2.20	0.130
1.83	2.20	0.223	3.00	3.33	0.387	1.67	2.33	0.069
1.83	2.33	0.114	3.00	3.17	0.718	1.67	2.17	0.114
1.83	2.33	0.114	3.00	2.67	0.432	1.67	2.67	0.070
1.83	2.33	0.114	3.00	3.00	1.000	1.67	2.17	0.241
1.83	1.83	1.000	3.00	3.50	0.226	1.67	2.17	0.241
1.83	2.17	0.218	3.00	3.17	0.718	1.67	2.00	0.387
1.83	2.00	0.405	3.00	3.50	0.201	1.67	2.17	0.114
1.83	2.33	0.206	3.00	2.83	1.000	1.67	2.00	0.387
1.83	2.17	0.487	3.00	3.17	0.485	1.67	2.33	0.069
1.83	2.67	0.056	3.00	2.33	0.177	1.67	2.33	0.069
1.83	2.33	0.114	3.00	3.17	0.718	1.67	2.50	0.070
1.83	2.50	0.054	3.00	3.17	0.718	1.67	2.17	0.114
1.83	2.33	0.114	3.00	3.00	0.787	1.67	1.83	0.784
1.83	3.00	0.025	3.00	2.83	0.718	1.67	2.17	0.542
1.83	2.50	0.054	3.00	3.17	0.718	1.67	2.17	0.114
1.83	2.00	0.405	3.00	3.33	0.654	1.67	1.83	0.784
1.83	2.33	0.114	3.00	3.00	1.000	1.67	2.83	0.039
1.83	2.00	0.405	3.00	3.00	1.000	1.67	1.83	0.595
1.83	2.00	0.673	3.00	3.33	0.387	1.67	1.83	0.595
1.83	2.33	0.114	3.00	3.33	0.432	1.67	2.83	0.039
1.83	2.50	0.054	3.00	3.17	0.733	1.67	2.67	0.018

Duramonte			Durafit			Byblos		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
3.17	3.33	0.863	2.67	2.33	0.311	2.50	3.00	0.548
3.17	3.33	0.584	2.67	2.33	0.311	2.50	3.80	0.036
3.17	3.50	0.527	2.67	2.67	0.929	2.50	3.83	0.020
3.17	3.00	0.787	2.67	2.67	0.793	2.50	2.17	0.588
3.17	4.00	0.033	2.67	2.67	1.000	2.50	3.17	0.115
3.17	4.33	0.087	2.67	2.80	0.724	2.50	3.50	0.123
3.17	3.67	0.112	2.67	2.67	0.929	2.50	3.33	0.276
3.17	3.50	0.282	2.67	3.83	0.020	2.50	4.00	0.065
3.17	3.17	0.930	2.67	2.33	0.437	2.50	2.33	0.718
3.17	3.50	0.282	2.67	2.50	0.640	2.50	3.50	0.123
3.17	3.33	0.924	2.67	3.00	0.541	2.50	3.50	0.123
3.17	3.33	0.595	2.67	3.50	0.241	2.50	3.67	0.040
3.17	3.33	0.584	2.67	2.33	0.523	2.50	3.00	0.356
3.17	3.17	1.000	2.67	3.17	0.784	2.50	3.50	0.123
3.17	3.33	0.584	2.67	2.33	0.437	2.50	4.00	0.009
3.17	3.33	0.595	2.67	2.67	0.793	2.50	3.67	0.019
3.17	3.50	0.285	2.67	2.50	0.794	2.50	3.50	0.218
3.17	3.33	0.584	2.67	2.33	0.523	2.50	3.33	0.120
3.17	3.33	0.595	2.67	3.00	0.541	2.50	2.17	0.432
3.17	3.33	0.545	2.67	2.50	0.640	2.50	2.67	0.923
3.17	4.33	0.024	2.67	2.83	0.931	2.50	3.67	0.019
3.17	3.33	0.924	2.67	2.50	0.794			
3.17	3.00	0.787	2.67	2.17	0.351			
3.17	3.83	0.100	2.67	2.17	0.417			

Nefer			Wimadur		
mean i.v.	mean PSVs	P-v.	mean i.v.	mean PSVs	P-v.
1.50	2.00	0.071	4.00	4.33	0.673
1.50	2.00	0.201	4.00	4.83	0.150
1.50	2.00	0.201	4.00	3.67	0.673
1.50	2.33	0.038	4.00	3.83	1.000
1.50	2.00	0.071	4.00	4.17	0.798
1.50	1.67	0.640	4.00	3.83	0.804
1.50	2.17	0.137	4.00	4.50	0.339
1.50	2.17	0.054	4.00	4.33	0.551
1.50	2.50	0.038	4.00	4.50	0.445
1.50	1.83	0.282	4.00	4.50	0.458
1.50	2.00	0.071	4.00	3.67	0.803
1.50	2.00	0.201	4.00	4.50	0.458
1.50	1.83	0.282	4.00	4.17	0.672
1.50	2.17	0.137	4.00	4.33	0.541
1.50	2.17	0.137	4.00	4.33	0.541
1.50	1.83	0.476	4.00	4.33	0.673
1.50	1.83	0.282	4.00	4.20	0.768
1.50	2.50	0.024	4.00	4.33	0.541
1.50	2.00	0.201	4.00	3.83	0.933
1.50	2.00	0.201	4.00	4.33	0.541
1.50	1.50	1.000	4.00	4.67	0.273
1.50	2.33	0.038	4.00	4.33	0.437
1.50	2.33	0.038	4.00	4.83	0.086
1.50	2.33	0.054	4.00	5.00	0.111