

# The importance of *Fusarium* head blight resistance in the cereal breeding industry: Case studies from Germany and Austria

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## Abstract

*Fusarium* head blight (FHB) resistance in wheat and triticale has a high priority in the European Union because of the strict guidelines for the major mycotoxins deoxynivalenol (DON) and zearalenone (ZON) and the admission policy of the regulatory authorities. Potentially 70% of the arable land in Germany and about 60% in Austria can be affected by *Fusarium*. Although epidemics occur only in some years and/or some regions, DON and ZON are detected every year in varying amounts in wheat, rye and maize. Despite a high significance of FHB resistance in breeding companies, as validated by a recent survey, breeding progress in wheat is basically absent for FHB resistance in both countries. The main reasons are the complex inheritance of FHB resistance and the high proportions of the dwarfing allele *Rht-D1b* in high-yielding varieties promoting susceptibility. Despite this, some varieties with high FHB resistance (score 2–3 on the 1–9 scale) have been released that account, however, only for 11% and 18% of the multiplication area in Germany and Austria, respectively. For triticale, an official testing system for FHB resistance in terms of DON content exists in Germany and Austria, but not for the other cereals. Susceptibility to maize ear rot has been described in Austria, but not in Germany. Additionally, a testing system for stalk rot resistance in both countries should be established.

## KEYWORDS

anther retention, deoxynivalenol, dwarfing genes, ear rot, maize, plant height, resistance, rye, triticale, wheat, zearalenone

## 1 | FUSARIUM DISEASES IN CENTRAL EUROPE

*Fusarium* species are unique because they occur in all continents (except Antarctica) and infect hundreds of plants from arabidopsis till zucchini. The major staple crops winter wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), and winter barley (*Hordeum vulgare* L.) that provide together with rice most of the world's food calories are hosts of

*Fusarium* diseases. Winter rye, winter triticale and oats are also among the affected crops. Giving the cultivation area, about 70% of the total arable land is potentially affected by *Fusarium* infections in Germany and about 60% in Austria (Table 1). This table also shows the high average grain yields in both countries. In winter wheat, the grain yield can rise up to an average of 91.5 dt/ha on a regional basis like in Schleswig–Holstein 2020 (DESTATIS, 2021).

The major *Fusarium* species in small-grain cereals are *Fusarium graminearum* sensu strictu (teleomorph *Gibberella zeae*, belonging to the *F. graminearum* species complex, FGSC) occurring worldwide,

† Deceased during the preparation of this manuscript.

**TABLE 1** Areas and grain yields of the most grown cereals in Germany and Austria averaged across 2020–2021 (DESTATIS, 2022; OESTAT, 2022).

Crop	Germany			Austria		
	Cultivation area		Grain yield (dt/ha)	Cultivation area		Grain yield (dt/ha)
	Hectares	In percent <sup>a</sup>		Hectares	In percent <sup>a</sup>	
Winter wheat	2,906,033	24.5	75.6	238,559	18.1	60.1
Silage maize	2,188,500	18.5	–	85,998	6.5	–
Winter barley	1,604,100	13.5	66.1	97,562	7.4	67.3
Winter rye	621,267	5.2	54.0	37,802	2.9	48.7
Grain maize	425,000	3.6	99.8	215,397	16.3	112.6
Winter triticale	332,367	2.8	58.9	53,081	4.0	55.8
Oats	167,600	1.4	44.6	22,248	1.7	39.2
<b>Total</b>	<b>11,846,700</b>	<b>69.5</b>		<b>1,320,425</b>	<b>56.9</b>	

<sup>a</sup>Relative to total arable land.

*F. culmorum* predominant in the cooler regions, *F. poae*, *F. avenaceum* and others. In maize, *F. graminearum*, *F. verticillioides*, *F. temperatum*, *F. subglutinans* and *F. proliferatum* (belonging to the formerly *Gibberella fujikuroi* species complex, now *Fusarium fujikuroi* species complex, FFSC) are occurring frequently in the temperate regions (Gräfenhan et al., 2011; Pfordt et al., 2020; Wigmann et al., 2019). The occurrence of the individual species depends on geographic and yearly weather conditions. Very often, several species occur on the same host in an epidemic.

The economically most important diseases in Central Europe are *Fusarium* head blight (FHB) of small-grain cereals and *Gibberella/Fusarium* ear rot in maize. In the US literature, maize ear rot caused by FGSC is called “*Gibberella* ear rot” (GER) and ear rot caused by FFSC is “*Fusarium* ear rot” (FER). All diseases do not only reduce grain yield but also grain quality because of a smaller grain weight, reduced technological quality and mycotoxin contamination. Mycotoxins occur in bread and breakfast cereals as well as in noodles, beer, maize-based food and feed stuff and cannot be inactivated by cooking or baking. They affect the whole value chain from farmers to producers (millers, maltsters, bakers and feed producers) to the consumer. Fungicides exist, mainly azoles (tebuconazol and metconazol), but their effectiveness is lower compared to that against powdery mildew or rusts, because they must be applied during or shortly after infection and infection mainly occurs during rainy periods. In maize, no fungicides are registered for the control of GER or FER in Germany. In Austria, 15 fungicides are released for hybrid seed production and three fungicides for farmer's use. Appropriate management techniques (no maize as pre-crop, tilling) and resistant varieties are important possibilities to combat *Fusarium* diseases in all crops especially when fungicide use should be minimised.

The *Fusarium* species produce different mycotoxins. Out of the mycotoxins regulated by the European Commission (EC), deoxynivalenol (DON) and zearalenone (ZON) are produced by *F. graminearum* and *F. culmorum*, fumonisins (FUM) by *F. verticillioides* and *F. proliferatum*, and T-2 and HT-2 toxins by *F. poae*, *F. langsethiae* and *F. sporotrichioides* (Johns et al., 2022). The other mentioned *Fusarium*

species produce different mycotoxins that are not regularly monitored like moniliformin by *F. avenaceum*, *F. subglutinans*, *F. proliferatum* or beauvericin by *F. temperatum*.

In Germany, FHB occurs only sporadically, because the appearance is greatly triggered by rainy weather during flowering/silking. Although only 2 mm rain are enough for FHB infection, this occurs not too often, and with the ongoing global warming, it might become even less frequent on a nationwide basis. Given their high plasticity, however, continuous adaptation of *Fusarium* populations to changing weather conditions can be expected, and a shift towards more thermophilic *Fusarium* species is likely (Miedaner & Juroszek, 2021).

Concerning Austria, the frequency of occurrence of FHB in the foothills of the Alps is similar to that in Bavaria, as they are in the same climatic region. The disease always occurs when it rains during flowering. In the south of Austria, FHB is always present in wheat because of the high proportion of maize in the crop rotation and the higher rainfall. However, the area under wheat is smaller there (about 5800 ha in Styria compared to 147,300 ha in Lower Austria in 2022). In the Pannonian region, on the other hand, rainfall is low, so major problems with FHB in soft wheat only occur every 8–10 years.

Important risk factors for infection are maize as previous crop, especially in combination with reduced soil management, and growing susceptible varieties. However, both diseases are a problem in many years on a regional basis when it rains just at flowering/silking time. And mycotoxins can also be found in varying amounts every year (see below). A yet underestimated disease is stalk rot of maize caused in Germany by *F. graminearum*, *F. equiseti*, *F. culmorum*, and *F. temperatum* (Pfordt et al., 2020).

## 2 | MYCOTOXIN REGULATIONS BY THE EU AND THEIR NATURAL OCCURRENCE

In the European Union (EU), the major problem raised by *Fusarium* infections is the mycotoxin contamination because of the strict

guidance and recommendation levels for human food for the major toxins (Table S1). For DON, ZON and FUM, the maximum levels for human food are legally binding (EC, 2007). For the sum of T-2 and HT-2, guidance levels are given, which are not binding. The latter also applies for all those mycotoxins in animal feed where the levels give only a guidance for risk management (EC, 2006).

Each year, the Max Rubner Institute for Safety and Quality in Cereals, Detmold, determines the occurrence and concentration of DON and ZON in harvest samples from wheat and rye collected for the 'Besondere Ernte- und Qualitätsermittlung (BEE)' (=specific harvesting and quality determination). A random selection of the samples takes place with selection probabilities proportional to the size of the selection units (farms). Varieties are selected proportionally to the area of the crop in this year. A fixed number of samples are examined from each federal state (Figure 1).

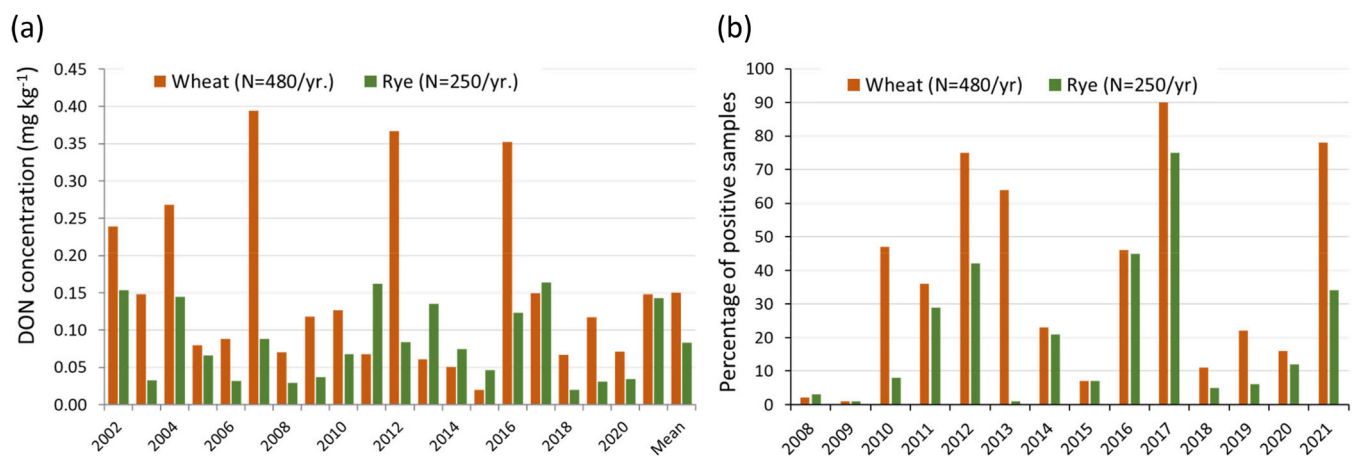
Although the mean DON concentrations of wheat and rye samples greatly varied among years, the percentage of positive samples is always very high (69–100%; BEE, 2010, 2021). Years with high mean concentrations for DON were 2007, 2012, and 2016 (Figure 1a). In these years, rainy weather during flowering occurred across many regions in Germany, promoting problems with mycotoxin contamination in elevators and mills. The gross average of DON was 0.150 and 0.083 mg kg<sup>-1</sup> for wheat and rye, respectively. This is lower than the results of a survey of *Fusarium* mycotoxins across European wheat, where the 10-year average of DON for food wheat was 0.358 mg kg<sup>-1</sup> and for feed wheat 0.858 mg kg<sup>-1</sup> (Johns et al., 2022).

Although the mean values in each year in Germany are far below the maximum levels given by the EU (Table S1), it must be admitted that the DON concentration of individual samples may be excessively high even in 'normal' years. For example, the most DON-contaminated wheat sample in 2020 and 2021 had 3.1 and 9.6 mg kg<sup>-1</sup>, respectively. However, only 0%–6% of the wheat samples and 0%–2% of the rye samples had higher DON concentrations than allowed for human food (1.25 mg kg<sup>-1</sup> DON; BEE, 2010, 2021). In most years, rye had a lower DON concentration than wheat.

The same samples are analysed for ZON (Figure 1b). Here, only the percentage of positive samples can be considered, because the mean concentrations are generally too low. Only 0 to 4 samples per year surpass the maximum levels of 0.1 mg kg<sup>-1</sup> for ZON. The most ZON-contaminated samples, however, had extremely high concentrations up to 1.1 mg kg<sup>-1</sup> for wheat and 1.5 mg kg<sup>-1</sup> for rye in 2017 and 2016, respectively (BEE, 2021). In most years, rye had a lower frequency of positive samples. A high dependence on the year is also found for ZON. However, not necessarily the same years like for DON concentration are affected illustrating that both mycotoxins are produced under different weather conditions. In years with a high abundance of toxins, the samples contained both DON and ZON. In the European survey, 25% of food and 45% of feed wheat samples containing DON were also positive for other *Fusarium* mycotoxins, mainly ZON and T-2 (Johns et al., 2022). The co-occurrence of ZON varied between 45% and 100% of the samples depending on the year.

In maize, weather exerts a significant influence on ear rot severity and toxin levels. Wet weather during flowering favours infection via the silk channel. Injury to the cob from hail and feeding damage from the European corn borer (*Ostrinia nubilalis*) provide entry points for fungal spores and exacerbate the problem. Wetness in September and October impedes water release from the kernels and allows fungal growth to continue longer, and increases toxin levels, especially DON.

DON concentrations are regularly analysed for grain maize in Bavaria. Here, natural infections in the State Variety Trials at two to three locations are analysed in three maturity groups with 12 to 34 varieties per group and three replicates (Figure S1a). Interestingly, the mean DON concentrations in maize are by about a factor of 10 higher than in wheat and rye although both analyses are from natural infections. This underlines the high general susceptibility of maize for ear rot. Again, the DON concentrations highly depend on the year and only a few years have high concentrations, especially 2010, 2014 and 2019. There is no tendency of higher/lower susceptibility according to the maturity group. Humidity during silking is the most important driving factor (Pfordt et al., 2020) that is, however, not correlated



**FIGURE 1** (a) Mean deoxynivalenol (DON) concentration in harvest samples of German wheat and rye from farmers' fields; (b) percentage of positive samples of zearalenone (ZON) in the harvest of German wheat and rye from farmers' fields (BEE, 2010, 2021). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

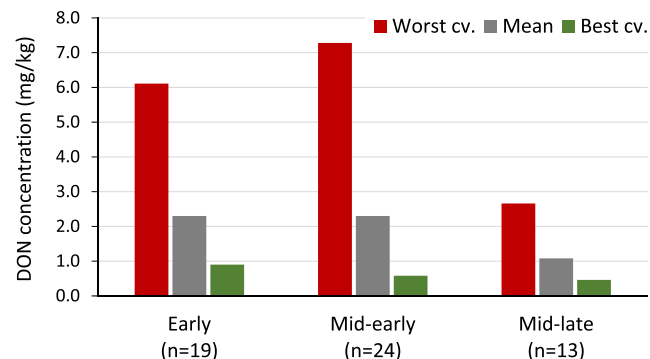
to maturity group. On average, the strict DON guidance level for feeding pigs (fattening pigs, breeding sows) of  $0.9 \text{ mg kg}^{-1}$  (EC, 2006) was reached or exceeded in six out of the 14 years analysed in at least one maturity group.

In Austria, pre-harvest monitoring of the mycotoxin content of grain maize has been set in place. Maize cultivated in the northeastern lowlands and hills is usually less contaminated with *Fusarium* toxins than when grown in the foothills of the Alps and the southern or southeastern growing regions. In 2014, frequent rainfall during the summer months caused extremely high DON levels (Figure S1b). Some batches were unsuitable for feeding and had to be utilized in biogas plants. Between the end of August and the beginning of October, official VCU (value for cultivation and use) trials and trials of the Chambers of Agriculture are sampled two to three times (Kauschitz et al., 2022) to detect a risk of elevated toxin levels in time and to react accordingly.

In the years with high average DON concentrations, like in 2019, a tremendous variation among the maize varieties was found in Bavaria (Figure 2) illustrating the genetic effect that could be used when GER is considered as a breeding target. The most susceptible cultivar had a 6- to 12-fold higher DON concentration than the most resistant cultivar. The most resistant cultivar was below the strict guidance level for pigs in all three cases, whereas the most susceptible cultivar did even exceed the high DON guidance level for feeding stuffs of  $5 \text{ mg kg}^{-1}$  for cattle (EC, 2006) in two maturity groups. Also in Austria, sensitive varieties show several times higher DON levels than low susceptible ones, especially in environments with higher ear rot severity.

### 3 | VCU TRIALS, THE CEREAL BREEDING INDUSTRY AND FHB RESISTANCE

In Europe, a national listing and plant variety protection are prerequisites for commercially trading agricultural species. National variety offices are responsible for these procedures. Plant breeders'



**FIGURE 2** Deoxynivalenol (DON) concentration of the worst and best cultivar (cv.) and the trial mean in harvest samples of grain maize in Bavaria from three maturity groups among two locations in 2019 ( $n$  = number of varieties tested; LfL, 2022). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

protection is granted for varieties that are distinct, uniform and stable (DUS testing), new and designated by a suitable denomination. It is an exclusive right, comparable to patent, which protect the intellectual property associated with plant breeding and can be applied for all varieties of plants. In contrast to patents, however, breeders are allowed to use all registered varieties for crossing and building-up new varieties (breeders' privilege). If a species is listed in the COMMON CATALOGUE OF VARIETIES OF AGRICULTURAL PLANT SPECIES ([https://food.ec.europa.eu/system/files/2022-03/plant-variety-catalogues\\_agricultural-plant-species.pdf](https://food.ec.europa.eu/system/files/2022-03/plant-variety-catalogues_agricultural-plant-species.pdf)), a national listing ('registration') is the prerequisite for marketing. The Seed act regulates that for national listing, varieties of agricultural species pass a test of the value for cultivation and use (VCU) in addition to the DUS test. The VCU is determined within a two to three years testing period (depending on the species) carried out at 10 to 20 locations. The approval for national listing requires that the qualities of the variety taken as a whole offer a clear improvement for cultivation, for use of the harvest or use of products derived from the harvest compared to comparable listed varieties. FHB resistance is an integral part of the VCU testing in Germany and Austria (AGES, 2022; BSL, 2022).

The German breeding industry consists of 58 private companies running own breeding programmes for agricultural and horticultural crops, 28 of these are engaged in cereal breeding (BDP, personal communication). In Austria, two private companies are active in breeding of small-grain cereals, and two others in maize breeding. Most companies are small to medium sized. Many companies, German and foreign-owned companies as well, have wheat breeding programmes in Germany, France, and the United Kingdom in parallel and exchange their genetic material across the countries. Most of the 20 independent wheat breeding programmes in Germany select for FHB resistance by artificial infections either by conidia suspension sprayed from above or by growing wheat after maize leaving the maize stubbles on the fields' surface or by natural infection.

An important factor for designing breeding goals by the companies is that the registration process in Germany and Austria includes FHB resistance for wheat and triticale. In Germany, the FHB scores in the Descriptive Variety List (BSL, 2022) are from special experiments with artificial spray inoculation across four to six locations per year and at least 3 years. In wheat, the visible symptoms are scored several times after inoculation in percent of bleached spikelets per plot and used for classification on a 1–9 scale with 1 = no symptoms and 9 = fully diseased (Table 2). The frequency of infected ears per plot (type I resistance) and the percentage of infected spikelet of an ear (type II resistance) are combined in one score. The publication of the scores is of great importance, because it gives farmers guidance in their choice of varieties, and it has a promotional function for the breeder. New varieties are released by the Federal Plant Variety Office in Germany only if they have a FHB score of  $\leq 6$  on the 1–9 scale. In the Bavarian and Hessian State Variety Trials, only varieties with a FHB score of  $\leq 5$  can enter.

In Austria, FHB resistance of common wheat, durum wheat and triticale are components of the VCU trials (BAES, 2015). FHB severity

**TABLE 2** All *Fusarium* head blight (FHB) resistant winter wheat varieties with score 2 and those with score 3 that have a multiplication area >300 ha and their agricultural performance<sup>a</sup> in comparison to the three most commonly grown varieties in Germany (BSL, 2022).

Cultivar	Year of release	FHB	Ear emergence	Plant height	Lodging tolerance	Grain yield	Baking quality <sup>b</sup>	Multiplication area (ha) <sup>c</sup>
Senaturo <sup>d</sup>	2017	2	6	8	6	6	A	6
Viki	2018	2	5	6	6	5	E	28
Opal	2011	3	6	5	4	5	E	700
Moschus	2016	3	5	5	4	5	E	835
Akasha	2021	3	6	4	5	7	B	528
Findus <sup>e</sup>	2014	3	4	5	5	6	A	381
<b>Most commonly grown varieties:</b>								
Asory	2018	4	5	4	6	7	A	3175
Chevignon <sup>e</sup>	2017	5	4	4	5	8	(B)	4569
RGT reform	2014	4	5	3	4	6	A	3211

<sup>a</sup>1 = highly resistant, very early, very short, highly lodging tolerant, very low yielding.

<sup>b</sup>Baking quality (in descending order): E, A, B, C.

<sup>c</sup>Multiplication area of the previous year (2021) as proxy for the importance of a variety.

<sup>d</sup>Tested on organic farming conditions.

<sup>e</sup>Released in another European Union member state.

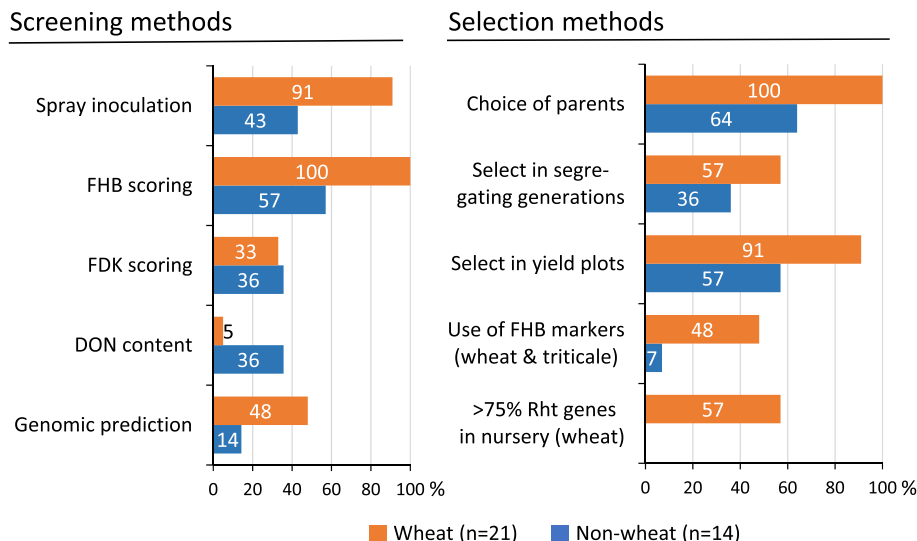
in wheat is also assessed on a 1–9 scale, however with a different classification than in Germany (Table 2; BAES, 2015). FHB susceptibility of winter and spring wheat are presented in the Descriptive List of Varieties since 1996. Initially, the observations were made exclusively in VCU trials under natural infection. In 2005/2006, an experiment with two variants was run: (1) spray inoculation at two locations with conidial suspension and (2) manually spreading of corn stalks at two locations. The latter method increases FHB infection pressure. It is a better option for experimental plots than performing reduced tillage after maize that may lead to technological problems in 10 m<sup>2</sup>-plot experiments. A support of infection by irrigation during wheat flowering is necessary. This approach mimics the natural infection pathway and includes the mechanisms of passive resistance. Therefore, it was decided to proceed in the VCU tests with this approach. For baking wheat, only varieties up to a maximum of FHB score of 6 are registered in Austria. For feed wheat, the FHB score up to 7 is not considered as an exclusion criterion, when the other traits are particularly favourable. Winter wheat varieties registered in Austria are described as one score more susceptible on average than in Germany depending on the differing rating scales (Table S2).

A recent survey of German and Austrian cereal breeders (questions, see Table S3a) showed that most respondents consider FHB resistance to be important or very important in their breeding programme. Only two spring barley and one oat breeder stated that they only practiced negative selection when natural infection occurred and one oat breeders totally denied the importance. Some breeding companies answered for up to five crops; winter and spring cereals were considered as two crops. The survey could be biased if only those breeders answered for whom FHB is important. However, FHB score is a variety acceptance criterion in both countries. Almost all wheat

breeders do spray inoculation followed by symptom scoring as also practiced in VCU tests (Figure 3). FDK is only analysed by a third of the wheat breeders, because this scoring is very laborious; DON content is routinely recorded by only one wheat breeder because of the high costs. Nearly half of wheat breeders use genomic prediction, which primarily may target grain yield and baking quality, but can also be used for FHB resistance when a representative training set is available. Among non-wheat breeders, four triticale breeders responded, five for barley, four for oats and one for rye (Table S3b). Because symptom scoring cannot reliably predict DON content in these crops (see below), FDK scoring and especially DON evaluation plays a much larger role in FHB evaluation than in wheat. Spray inoculation is also used much less than in wheat, probably because other *Fusarium* species often infect here, which are not so easy to handle. One rye breeder also uses relative yield loss as a measure of resistance. A lower percentage for genomic prediction most likely results from the lower monetary revenue for these crops.

Regarding selection methods, parental selection plays a central role for all wheat breeders. About half of them also select in the segregating generations or among doubled haploid (DH) lines. On the other hand, 91% of wheat breeders use yield testing plots simultaneously for selection of FHB resistance. FHB markers, primarily for *Fhb1*, are used by about half of the wheat breeders (and one triticale breeder). Nearly 60% of wheat breeders report that their breeding material contains more than 75% dwarfing genes, which has a significant (negative) impact on FHB resistance (see below). Interestingly, both Austrian wheat breeders responded that *Rht* genes play no or a minor role in their programmes. Among non-wheat breeders, the frequencies for using specific selection methods were lower because some of them do not select intensively for FHB.

**FIGURE 3** Results of a survey among German and Austrian cereal breeders ( $n_{\text{total}} = 35$ , companies  $\times$  crops). DON = deoxynivalenol; FHB = Fusarium head blight; FDK = Fusarium damaged kernels; Rht = reduced height. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



#### 4 | BREEDING PROGRESS AND CHALLENGES FOR SELECTION OF FHB RESISTANCE IN WHEAT

Data from the German Federal Plant Variety Office are from the official test for the value of cultivation and use (VCU). We analysed only those entries that were later registered as varieties. Least square means for varieties were estimated adjusted for years (Laidig et al., 2008). For the Austrian VCU trials, the original data were used. Data are highly unbalanced because each variety is regularly tested for 3 years, and in each cycle of 3 years, different varieties are tested. Only a few standard varieties are grown throughout the years.

The breeding progress of a trait over years demonstrates the success of the breeders in the improvement of this trait. No substantial genetic breeding progress could be demonstrated in Germany for FHB resistance across the last 20 years (Figure 4a). Calculated after the method of Piepho et al. (2014), the non-genetic trend (green line) was +1.3% FHB severity per year and the genetic progress (red line) was −.25% per year only. This negative genetic trend was caused by the highly susceptible cultivars registered in 2002–2008. Because the data have been weighted for the trial year and the number of locations, the high non-genetic variation is mainly because of the effect of variable weather conditions during anthesis on the infection. The upward non-genetic trend therefore shows that in recent years the conditions for FHB infection have become more favourable.

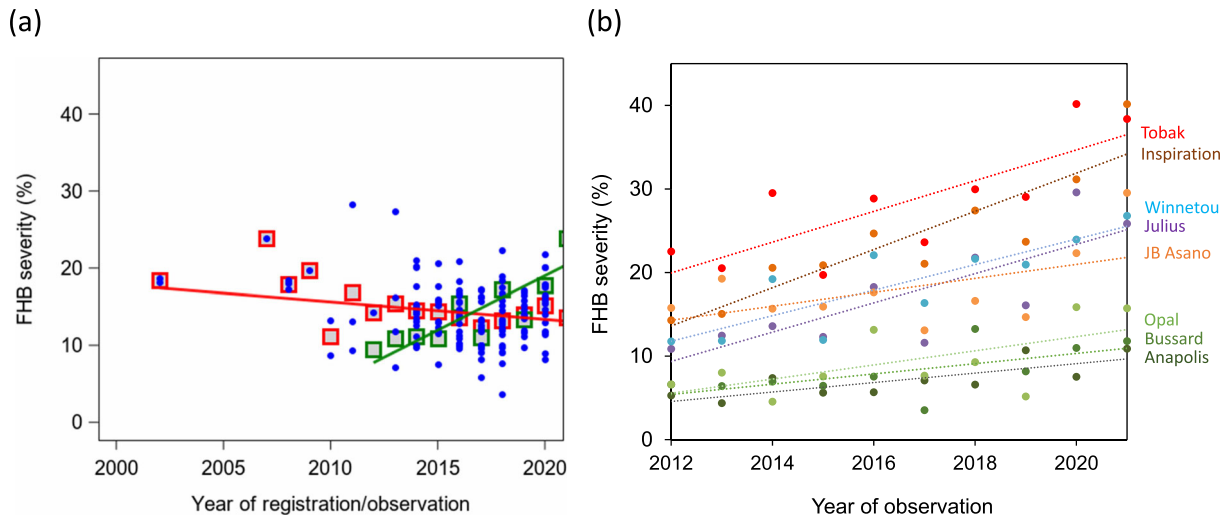
Even though it takes a lot of effort to breed resistant varieties, the resistance achieved proved to be durable (Figure 4b). Especially the most resistant varieties in these trials (‘Anapolis’, ‘Bussard’ and ‘Opal’) were the most stable ones, that is, had the smallest standard deviations across years and did not considerably change their FHB severity across 10 years although they were grown on large acreages. For ‘Bussard’ (released in 1990), this holds true even for 20 years where the cultivar did not change its FHB score of 3 in the official Descriptive Variety List. Again, the non-genetic trend with higher

FHB severity in the last years of observation can also be seen in this graph. Moreover, the more susceptible varieties tend to be less stable across years, that is, they are more affected by changing infection conditions than the resistant varieties.

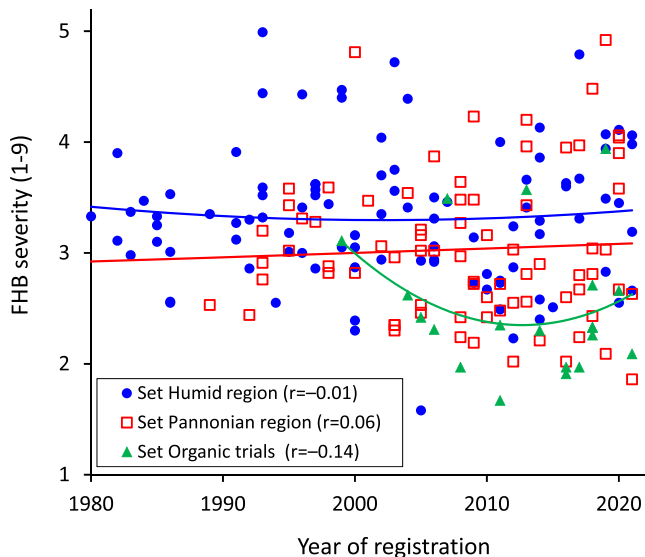
For the three sets of trials from the Austrian VCU test also no breeding progress can be detected (Figure 5), although this series extends over a longer period of time. Irrigation of the experiments effectively standardised FHB infection pressure. Therefore, different locations showed high rank correlations ranging from  $r = .63$  to  $.84$  in the period from 2016 to 2022 (Flamm, personal communication). In contrast, an analysis of 1068 genotypes from nurseries in the northern USA reported moderate but significant genetic breeding gains of 1.56 and 1.41% per year for FHB severity and DON reduction, respectively (Gaire et al., 2022). However, it is not known which of these genotypes are actually grown in practice, that is, it is not clear whether this progress could be transferred to farmers.

The missing breeding progress for FHB resistance in Germany and Austria is illustrated by the fact that the recently released varieties do not show a lower mean FHB susceptibility in comparison to the old varieties. This is astonishing because most large wheat breeding companies have their own FHB resistance tests every year (Figure 3). The causes are manifold and cannot simply be overcome:

- Quantitative resistance: many minor resistance loci in European materials
- High importance of genotype-by-environment ( $G \times E$ ) interaction
- No major FHB quantitative trait loci (QTL)/genes from non-adapted origin in released cultivars
- Morphological factors counteract breeding success:
  - Lateness and tallness are (indirect) resistance factors
  - Short *Rht-B1* and *Rht-D1* alleles specifically enhance FHB susceptibility
- Many other breeding goals have to be fulfilled, for example, in winter wheat, 28 traits are given in the German Descriptive List of Varieties; in Austria, even 42 traits are considered



**FIGURE 4** Fusarium head blight (FHB) severity of winter wheat varieties plotted against the year of registration of (a) 158 varieties registered after year 2000 and tested within the German VCU test after artificial infection from 2012 to 2021, weighted for the number of locations ( $n = 4-6$ ), blue dots: adjusted variety means, red squares with grey filling: adjusted group means of varieties, that is, groups of varieties with the same registration year corrected for year of observation, green squares with grey filling: adjusted annual means corrected for varieties plotted against the year of observation, red line: genetic trend, green line: non-genetic trend; (b) annual means of FHB severity of eight varieties tested in 10 years within the German VCU after artificial infection from 2012 to 2021; per year 4–6 locations were available (a and b same data source: German Federal Plant Variety Office). FHB, Fusarium head blight; VCU, value for cultivation and use. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 5** FHB severity of winter wheat varieties plotted against the year of registration of 198 varieties from the Austrian VCU test from 1985 to 2022 (Data source: AGES). FHB, Fusarium head blight; VCU, value for cultivation and use. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

- In the VCU trials also rather susceptible varieties show up regularly and are sometimes registered for other reasons (Figures 4 and 5).

A main cause for the missing breeding progress is the complex inheritance of FHB resistance in all European cereals. The quantitative phenotypic distribution (Figure 6) implies a polygenic inheritance by many minor loci and a high importance of genotype  $\times$  environment

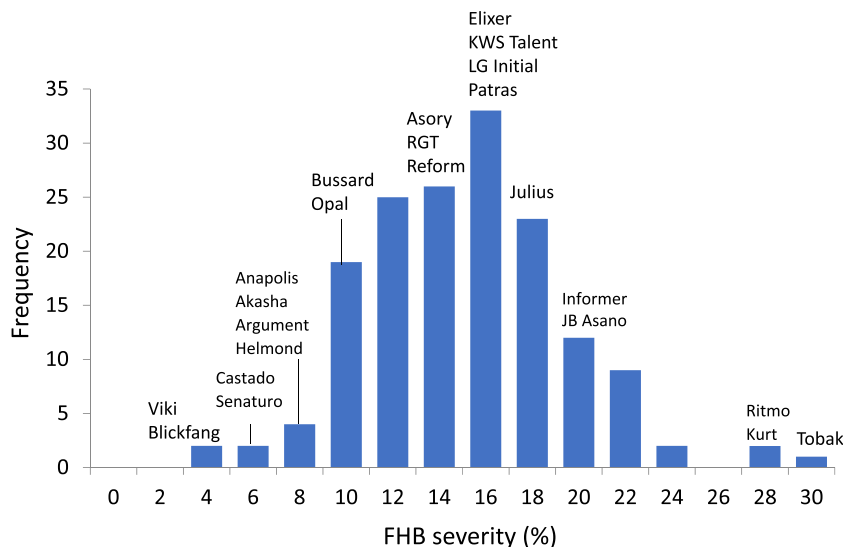
interaction in wheat and maize as well (e.g., Bolduan et al., 2009; Buerstmayr et al., 2020; Steiner et al., 2019). The former has since been confirmed by many QTL studies (Venske et al., 2019). Success from phenotypic recurrent selection was, therefore, restricted to 6%–10% per cycle (Jiang et al., 1993; Miedaner et al., 2009; Wilde et al., 2007; Yang et al., 2000).

Figure 6 clearly shows that from the registered varieties only two are rather resistant and five are highly susceptible, and the majority is moderately resistant to moderately susceptible. A similar picture can be derived from the Austrian Descriptive List of Varieties. Among the 79 varieties registered in Austria, 14 have low levels of susceptibility (score 3), 30 varieties have score 4, 14 varieties score 5, 18 varieties score 6 and 3 varieties score 7 (AGES, 2022). According to the quantitative inheritance of FHB resistance, no cultivar without any symptoms (0% or score 1) is expected.

Moreover, the FHB genes from exotic sources, like *Fhb1* – *Fhb7*, are not used in any released varieties to date because of concerns that the high grain yield levels will be reduced by pleiotropically acting non-adapted FHB resistance genes. A previous paper could demonstrate this only to a limited extent with 2% to 4% reduction in grain yield because of the incorporation of *Fhb1* and *Fhb5* (von der Ohe et al., 2010). However, a difference of 5% in grain yield corresponds to one score in the Descriptive List of Varieties and may restrict the use of this variety by the farmers.

Another complex hindering breeding progress for FHB is the role of morphological factors, especially lateness and tallness that are indirect resistance factors (Figure S2). A moderate negative correlation between flowering date and FHB severity ( $r = -.33$ ) and a higher negative correlation between plant height and FHB severity ( $r = -.62$ )

**FIGURE 6** Quantitative inheritance of Fusarium head blight (FHB) severity of 160 registered varieties tested within the German VCU test after artificial infection from 2012 to 2021 weighted for the respective trial year and the number of locations ( $n = 4\text{--}6$ ); some standard varieties are named (Data source: German Federal Plant Variety Office). VCU, value for cultivation and use. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



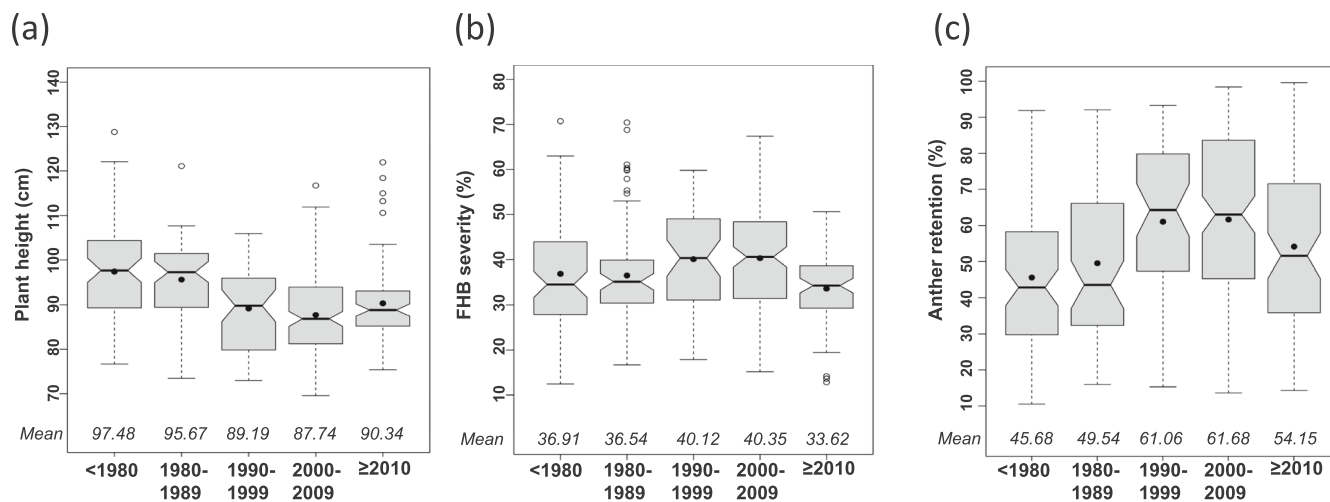
were found in a comprehensive European winter wheat diversity panel of 420 varieties. The first correlation was not affected by the respective reduced height (*Rht*) gene, but the later genotypes often show a lower FHB severity. Because lateness is not a desirable breeding goal, this correlation reduces breeding progress to a certain extent. In the Austrian VCU trials, no clear association between the date of ear emergence and FHB severity was found.

The negative correlation plant height – FHB severity has several aspects (Mao et al., 2010). Firstly, tallness is clearly a resistance factor, and tall genotypes tend to be more resistant (Buerstmayr et al., 2020). This is coherent with QTL and association mapping where in about 40% of all studies a co-segregation of QTL for FHB severity and plant height were reported (Buerstmayr et al., 2020). Secondly, the negative effect of the *Rht-D1b* allele (and its homoeologous counterpart *Rht-B1b*, both together called *Rht-1b*) on FHB severity has been reported frequently (Buerstmayr et al., 2020; Srinivasachary et al., 2009; Voss et al., 2008). The cause is a mutated DELLA protein reducing the sensitivity to gibberellic acid and thus plant height, and also enhancing Type 1 susceptibility (initial infection) to FHB relative to the wild type (Nicholson et al., 2008; Saville et al., 2012). In Figure S2b, both causes are considered: (i) the analysis of tall genotypes without a *Rht-D1b* allele ('None') show that the effect of tallness per se is still significant ( $r = -.42, P < .001$ ), (ii) genotypes with the *Rht-D1b* allele are clearly more susceptible. *Rht24b* alone had no effect on FHB resistance (Miedaner, Lenhardt, et al., 2022). Short-strawed wheats are favoured in intensive European agriculture because of their ability to convert higher nitrogen inputs into higher grain yields without lodging, the negative effect of these short *Rht-1b* alleles is considerably reducing selection gain for FHB resistance. Large populations are necessary to find short, resistant progenies (Voss et al., 2008). When progenies were selected only for FHB resistance, they turned out to be, on average, considerably taller than the population mean (Herter et al., 2019).

An interesting alternative for selection is the determination of the anther retention/anther extrusion, because a high anther retention is

positively correlated with FHB severity (Lu et al., 2013). The hypothesis here is that the anthers remaining in the floret provide a nutritional base for the fungus that facilitates and accelerates *Fusarium* infection. Moreover, in the meantime, we know that *Rht-B1b* and *Rht-D1b* both increase anther retention (Buerstmayr & Buerstmayr, 2016) that might be an important part of the dwarfing gene's enhancement of FHB susceptibility. A recent path analysis within the European winter wheat diversity panel showed that the morphological factors plant height and anther retention have a narrow genotypic correlation with FHB severity ( $r_g = -.64$  and  $.74$ , respectively) and explain together 67% of the phenotypic variation for FHB severity (Akohoue et al., 2022). A 1% higher anther retention caused a 0.57% higher FHB severity. It could, therefore, be advantageous for the breeder to select firstly genotypes having the lowest anther retention (=highest anther extrusion), thus exploiting the high direct path and positively pleiotropic loci between FHB severity and this trait. This is easy and cheap to perform even in large populations and does even not need a *Fusarium* infection.

When comparing the *Rht* genes in a European winter wheat diversity panel registered over five decades, it can be clearly seen that the frequency of the dwarf *Rht-D1* allele increased very much (Figure S3). It was used till 1989 in about 20% of the varieties and nowadays is used in more than 70% of all cultivars either alone or in a combination with *Rht24b*. This high frequency of the FHB-enhancing *Rht-D1b* contributes to the missing breeding success for FHB resistance. Accordingly, with the increasing percentages of *Rht-D1b* plant height decreased, FHB severity and, even more, anther retention increased (Figure 7). This illustrates the effect of *Rht-D1b* on the mentioned traits. Without the targeted selection for FHB resistance, there would have been a much greater increase in *Fusarium* susceptibility with the increasing frequency of *Rht-D1b* in the varieties than observed. In the last decade, plant height increased by 2.6 cm on average, and accordingly FHB severity and anther retention decreased what might be due to the even higher impact of the breeders on FHB resistance.



**FIGURE 7** Boxplots of (a) plant height, (b) FHB severity, and (c) anther retention of a European winter wheat diversity panel with varieties registered in different decades as shown in Figure 11 (a, b: Miedaner, Lenhardt, et al., 2022; c: unpublished data). FHB, *Fusarium* head blight.

The negative correlation of FHB severity with plant height can also be seen in the three Austrian sets of varieties, although in Austria, semi-dwarf cultivars are not common (Oberforster, 2022; Morales et al., 2022; Figure 8).

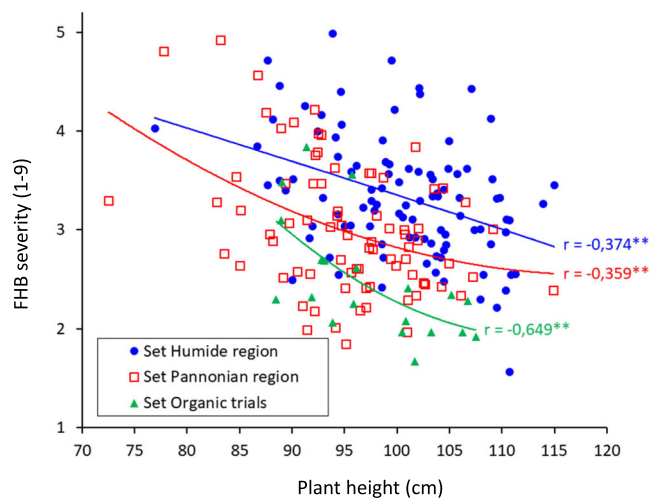
Both morphological factors, heading or flowering stage/date and plant height, can be statistically neutralised for selection by using them as covariate in the analyses (Miedaner, Flath, et al., 2022) or by setting thresholds with minimum requirements for both traits (Herter et al., 2019).

For the breeder, the correlation of FHB symptoms and DON content is a critical parameter, because the DON content is very laborious and expensive to determine. In wheat, the correlation between FHB symptoms and DON content is fairly high in artificially infected plots ( $r \approx .8$ , Miedaner et al., 2004). It is reported that the correlation between *Fusarium*-damaged kernels (FDK) and the DON content is also high (Mesterházy, 2020).

## 5 | DESPITE A LOW BREEDING PROGRESS, SUPERIOR WHEAT CULTIVARS ARE AVAILABLE

Together with the fact that many other breeding goals have to be achieved for the registration of commercial varieties, the reduced breeding success for FHB resistance results either in only low to moderate FHB resistance of successful varieties or in FHB-resistant but less competitive varieties (Tables 2 and 3).

The most FHB-resistant varieties ‘Senaturo’ and ‘Viki’ in the German Descriptive Variety List (Table 2) have basically no multiplication area. ‘Senaturo’ and the quantitatively resistant varieties with score 3 often have a lower grain yield. For varieties with baking quality E, A and B, the maximum grain yield in the list is 6, 8 and 9, respectively. The commercially most grown varieties on the other hand have a FHB score of 4 to 5 which is not bad and also



**FIGURE 8** Association between Fusarium head blight (FHB) severity and plant height for 198 varieties from three trial series of the Austrian VCU test. \*\*Significant at  $P < .01$  (Oberforster, 2022). VCU, value for cultivation and use. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

not excellent. Both scores are insufficient when several risk factors come together.

In Austria, 14 out of the 75 winter wheat varieties listed in the Descriptive Variety List 2022 are classified as low susceptible (score 3). These include, for example, ‘Adamus’, ‘Albertus’, ‘Arminius’, ‘Edelmann’, ‘Ehogold’, ‘Mandarin’, ‘Midas’, ‘Monaco’, ‘Tilliko’ and ‘Tobias’ (Table 3). Similar to Germany, the best FHB-resistant cultivars are not the most grown ones but have a higher impact in commercial farming than in Germany. Cultivars with score 2 do not exist in Austria.

Combining the FHB scores of winter wheat varieties in the German Descriptive List of Varieties with the seed multiplication area (Figure S4a) shows that only 11% of the varieties are in class 3, and the majority has scores 4 and 5. Two varieties are in FHB rating class

**TABLE 3** Fusarium head blight (FHB) resistant winter wheat cultivars with the best score 3 that have a multiplication area >100 ha and their agricultural performance<sup>a</sup> (AGES, 2022) in comparison to the most grown cultivars in Austria.

Cultivar	Year of release	FHB	Ear emergence	Plant height	Lodging tolerance	Grain yield <sup>b</sup>	Baking quality <sup>c</sup>	Multiplication area (ha) <sup>d</sup>
Arminius <sup>e</sup>	2016	3	4	7	6	5/5	7	246
Edelmann <sup>e</sup>	2017	3	5	6	7	5/4	7	114
Monaco	2019	3	4	4	3	6/–	7	113
Tobias <sup>e</sup>	2011	3	6	7	5	3/3	8	117
<b>Most grown cultivars:</b>								
Aurelius	2016	6	4	5	3	6/6	7	490
Capo	1989	4	5	7	7	4/3	7	524
Christoph	2018	7	4	3	3	5/5	7	490

<sup>a</sup>1 = highly resistant, very early, very short, highly lodging tolerant, very low yielding.

<sup>b</sup>Pannonian region/humid region.

<sup>c</sup>Baking quality 1 = very low baking quality, 9 = very high baking quality.

<sup>d</sup>Multiplication area of the year 2022 as proxy for the importance of a variety.

<sup>e</sup>Tested on organic farming conditions.

2 (=0.08%), four varieties in class 6 (=0.15%) and one in class 7 (=0.05%; BSL, 2022). In Austria, varieties with score 3 were grown on 17% of the seed multiplication area (excluding EU varieties), and most varieties are classified in FHB score 4. The highly susceptible (score 7) wheat varieties ‘Christoph’, ‘Frenetic’ and WPB ‘Calgary’ are grown on 13% of the multiplication area (Figure S4b).

## 6 | DETECTION OF FHB RESISTANCE IN OTHER CEREAL CROPS

The survey among cereal breeders revealed that the consideration of a resistance trait by variety offices is a strong motivation for private plant breeders to pursue resistance breeding. *Fusarium* resistance is further described in Germany for FHB in triticale and stalk rot in maize. In Austria, it is considered for variety approval of triticale and durum wheat and for ear rot of maize.

In triticale ( $\times$ *Triticosecale*), FHB resistance breeding is also a challenge. Because triticale is used only for feed, *Fusarium* mycotoxins greatly affect feed quality, especially when fed to swine. In a large panel of 656 triticale varieties, significant ( $P < .01$ ) correlations between FHB severity and heading date ( $r = .35$ ) and plant height ( $r = -.19$ ) occurred (Miedaner, Flath, et al., 2022). The latter correlation might be so low, because dwarfing genes are not commonly used in triticale to date. Basically, triticale has a similar FHB severity like winter wheat. The correlation between symptom rating and DON content, however, is on a much lower level with  $r = .32$  for FHB rating and  $r = .57$  for FDK among 150 DH lines (Miedaner et al., 2016). Therefore, the Plant Variety Offices of Germany and Austria use only the DON content measured by a commercially available enzyme-linked immunosorbent assay (ELISA) for the classification of triticale varieties from inoculated VCU tests (BSL, 2022). In Austria, three to five locations are used for testing, partly inoculated with the maize stubble method. The distribution of FHB severity among released

cultivars is rather similar in Germany and Austria ranging from score 3 to score 6 or 7 (Figure S5). In both countries, more resistant cultivars (score 2) are missing.

Durum wheat (*Triticum turgidum* ssp. *durum*) is known to be more sensitive to infection by *Fusarium* fungi than common wheat (Steiner et al., 2019). Effective resistances have not yet been found in this cereal. Frequent rainfall at the flowering stage of the plants can also lead to serious FHB infection even after ploughing or after previous crops that are not considered being critical for FHB, such as rapeseed, potato or sunflower. Because durum wheat is grown in Austria mainly in the low-rainfall Pannonian region, the production risk is nevertheless manageable in most years. In Austria, spring durum varieties have been classified in this trait since 1996, and those of winter durum since 1999. Differences are much lower than for common wheat varying from score 6 (moderate to severe) to score 8 (severe to very severe). As with common wheat, breeding progress is lacking.

FHB resistance is also a breeding issue among the other small-grain cereals rye, barley and oats. However, there is no official VCU testing in Germany and Austria, so there is little data on the performance of actual breeding material. In principle, resistance in these hosts is also inherited quantitatively with a combination of QTL with major and minor effects. However, some issues are different from those in wheat and should be briefly mentioned here. Firstly, the spectrum of *Fusarium* species and consequently their produced mycotoxins are different. Nielsen et al. (2011) found in Denmark that *F. graminearum*, *F. culmorum*, and *F. avenaceum* were dominant in wheat, triticale, and rye with DON as the most important mycotoxin, whereas in barley and oats, *F. langsethiae* replaced *F. graminearum* as the most important species leading to high levels of T-2 and HT-2. In Germany, additionally *F. sporotrichioides* was found in barley (Linkmeyer et al., 2013). Secondly, symptoms are difficult to assess in the field for a variety of reasons (see below), and thirdly, often no specific foreign sources of resistance are reported; resistant material has to be detected within the own breeding populations.

In winter rye (*Secale cereale* L.), FHB infections generally occur at a much lower incidence than in wheat, and accordingly, the reported DON and ZON levels are lower in most years (see Figure 1). There are several reasons for this. The most important is the much taller growth of rye compared to short-strawed wheat (approximately 1.5–1.6 m vs. 0.7–1.0 m). In addition, all cultivars are heterozygous and therefore represent different genotypes with potentially different susceptibilities, semi-dwarf genotypes are still absent, the anther extrusion is maximal because of the outcrossing nature of rye and the two-rowed head is less dense with a greyish thick waxy layer (Gaikpa, Lieberherr, et al., 2020). In this study, durum and bread wheat cultivars accumulated on average 67% and 39% more DON than rye, confirming the data shown in Figure 1. In a larger breeding population, high genetic progress through recurrent selection for FHB resistance was found (Gaikpa, Koch, et al., 2020), which could be partially explained by a high-effect QTL. Similar to triticale, visual symptoms in rye are not as easy to quantify as in wheat because of the heterogeneity of cultivars and the light blue–green colour of the head. Therefore, in the breeders' survey, one rye breeder wrote that, in addition to symptoms, he also analysed the grain yield of inoculated plots compared to non-inoculated controls.

In barley (*Hordeum vulgare* L.), visual assessment of symptoms at low infection pressure is very difficult because symptoms are restricted to individual spikelets and there appears to be no movement of the fungus within the ear through the rachis. Therefore, infected kernels are counted either two to three weeks after inoculation or after harvest and calculated relative to the total number of spikelets resembling FDK rating in wheat. This is an increased workload and limits the size of populations analysed in practical breeding. As a result, only one in five barley breeders uses spray inoculation in the field with DON analysis, whereas the others rely on natural infection and kernel evaluation after harvest. In Germany, natural infection is highly variable from year to year. Of particular concern is *Fusarium* infection in spring barley, as the beer might be prone to gushing and the mycotoxins are transferred to the beer during the brewing process. The Swiss cultivar 'Chevron', which is widely used in US barley breeding, is not used in Germany because of its low grain yield, weak straw and high susceptibility to foliar diseases (Linkmeyer et al., 2013).

Similarly, in oats (*Avena sativa* L.), symptom assessment in the field is almost impossible because of the weak symptoms and the peculiar structure of the panicle. Because of the long distances between spikelets within a panicle, no movement of the mycelium within the panicle is expected (Herrmann et al., 2020). Again, FDK assessment is the most practical solution, but even on the grain the symptoms are difficult to see because of the tight husks. Mycotoxin analysis is also a possibility, but because of the complex *Fusarium* population, including *F. poae* in Switzerland, the focus should be clearly on T-2 and HT-2 mycotoxins (Schöneberg et al., 2018). A significant variation in DON and T-2 levels was found among 25 oat genotypes in Germany, with the dwarf genotype 'Troll' having by far the highest toxin content (Herrmann et al., 2020). The genetic basis of dwarfism in this cultivar is the *Dw6* gene, which may be pleiotropically responsible for *Fusarium* susceptibility. The four oat breeders who responded

our survey relegated selection for *Fusarium* resistance to pre-breeding, because there are still too many uncertainties about *Fusarium* species and toxins, or because field selection is hardly possible. FHB resistance is especially important for breeders that are acting on the Scandinavian or British market.

In summary, for the small grain cereals other than wheat, symptom expression is difficult to assess in the field. Even though FHB can be important in these crops, not all breeders see the need for resistance selection, as testing is very laborious; no official VCU testing takes place and resistant varieties are thus not widely promoted.

In maize, also no official ranking of the genotypes for ear rot is given by the Federal Variety Office in Germany. For stalk rot, scores are published, but because they are from natural infections they have only a restricted variation from score 2 to 4 (BSL, 2022).

In Austria, maize varieties have been described in terms of their susceptibility to ear rot since 2011. Until 2021, artificial infection was conducted via two methods mimicking the two natural ways of infection. For the silk-channel inoculation, a conidium suspension was injected in the silk channel about 6 days after silking at one location with two replicates. For kernel inoculation, the cob was punctured with needles previously immersed in conidium suspension at two locations with two replicates. Scores are visually assessed as the area of the ear affected. DON surveys were not conducted here. However, these trials were terminated in 2022, and only natural infection is observed in the VCU tests since then.

Currently, maize varieties are rated from score 3 (low susceptibility) to score 7 (high susceptibility) for ear rot (Figure S6). As in the other crops, differences among varieties are quantitative. No preference of individual maturity groups is given what is similar to the maize mycotoxin data (Figure S1). The inheritance of *Fusarium* ear rot in maize is also caused by many low-effect QTLs that are population and environment specific for the most part (Akohe & Miedaner, 2022; Gaikpa & Miedaner, 2019).

High correlations between maize ear rot symptoms and DON and ZON concentrations after artificial infection ranging from .86 to .96 were reported for silk-channel inoculation of *F. graminearum* or *F. verticillioides* (Löffler et al., 2010). In a later study, this correlation was confirmed (Miedaner et al., 2015). For DON concentration measured by ELISA, a narrow correlation to near-infrared spectroscopy (NIRS) data was found ( $r = .93$ ). The NIRS values for DON could even predict the ZON concentration ( $r = .71$ ) in this study, because the concentration of both mycotoxins was also tightly correlated ( $r = .93$ ). This might be caused by the artificial infection with one isolate producing both mycotoxins in this study and may not represent natural infections where many isolates and often several *Fusarium* species are involved.

## 7 | HOW TO PROCEED IN FUTURE RESISTANCE BREEDING

Because FHB resistance in European cereals is governed by many low-effect QTL, genomic selection could be a recommended modern

technique for trait improvement. Previous papers revealed an appreciable prediction ability in wheat, triticale and rye (Arruda et al., 2016; Herter et al., 2019; Gaikpa, Koch, et al., 2020; Galiano-Carneiro et al., 2019). All these studies showed that marker-assisted selection (MAS) is clearly inferior to genomic selection (GS). A comparison of five selection methods in durum wheat (Steiner et al., 2019) showed a rather high prediction ability by phenotypic selection that was only overcome by genomics-assisted selection, that is, a phenotypic selection followed by GS, that increased prediction ability by 4% (Figure S7). The advantage of phenotypic over two genomic-based selection methods was 40% in terms of prediction ability. Genomics-based selection without and with using the most promising markers as fixed effect (= enhanced genomic-based selection) were still better than MAS. Accordingly, phenotypic selection was clearly superior over MAS in an earlier study in durum wheat and had also a better prediction ability than genomic-based selection (Miedaner et al., 2017).

To consider the negative correlations between FHB resistance and flowering date or plant height, a multi-trait GS should be applied (Moreno-Amores et al., 2020). With this advanced methodology, higher breeding success and a better agronomic performance of the resulting FHB-resistant varieties should be given in the future, because also other traits can be integrated in the multi-trait GS model. In a preliminary publication, Morales et al. (2022) compared different GS models for German, Austrian and Norwegian winter wheat. The highest prediction ability was found for GBLUP + AnthesisDate + *Rht-D1* (PA = 0.87 ± 0.03), followed by GBLUP + AntherRetention + *Rht-D1* (PA = 0.84 ± 0.04) in a fivefold cross-validated procedure. This again highlights the importance of integration of morphological traits for FHB resistance that was also reported elsewhere (Akohoue et al., 2022; Buerstmayr & Buerstmayr, 2016; Lu et al., 2013).

Genomic selection would be especially valuable for barley and oat where the symptom assessment in the field is practically not possible. To result also in less mycotoxin-accumulating varieties, a respective test should be done in all crops during the last selection step before the application for registration. In Germany, it would be important to test ear rot resistance of maize in multi-locational trials like for FHB resistance in wheat and to communicate it to the farmers via the Descriptive Variety List. For both countries, additionally a testing system for stalk rot resistance in maize should be established in the future to motivate breeders to select for more resistant varieties.

#### AUTHOR CONTRIBUTIONS

TM conceived the topic and wrote the manuscript for the data from Germany, MO contributed the data from Austria, and CF finished the collection of Austrian data because of the death of MO during the preparation of this manuscript. TM and CF read and approved the final manuscript.

#### ACKNOWLEDGEMENTS

Special thanks are due to Dirk Rentel and Dr. Carolin Lichthardt from the German Federal Plant Variety Office who provided the data of

Figures 4 and 6 and critically reviewed the paper, and to Dr. Friedrich Laidig, University of Hohenheim, Unit of Biostatistics, who did the statistical analyses for these data and all breeders who have replied to our questionnaire. We also want to thank Silvia Koch, University of Hohenheim, for statistically analysing the reported data from the European winter wheat diversity panel. Open Access funding enabled and organized by Projekt DEAL.

#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data availability statement does not apply because this is a review paper.

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#### SUPPORTING INFORMATION

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

**How to cite this article:** Miedaner, T., Flamm, C., & Oberforster, M. (2024). The importance of *Fusarium* head blight resistance in the cereal breeding industry: Case studies from Germany and Austria. *Plant Breeding*, 143(1), 44–58. <https://doi.org/10.1111/pbr.13098>