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Relationship between genetic variability of flowering traits and *Fusarium* mycotoxin contamination in oats

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Abstract

Over the last three decades, *Fusarium* infections and related mycotoxin contamination have caused significant economic losses in oats (*Avena sativa* L.). Breeding for resistance is highly prioritized in oats, but infection processes and resistance components against *Fusarium* species are not fully identified. In this study, the genetic variation for flowering traits and its impact on mycotoxin accumulation in oats is described. The first experiment of this paper was focused on flowering traits in 50 oat genotypes (Panel 1) to identify cleistogamic oats. Then, two separate *Fusarium*-inoculated experiments in three (Panel 2 with 25 genotypes) and two environments (Panel 3 with 16 genotypes) were conducted to assess the relationship between the degree of anther retention (AR) and resistance to *Fusarium* infestation and mycotoxin accumulation in oats. Panel 2 was inoculated with *Fusarium culmorum*, *F. langsethiae*, and *F. sporotrichioides*, and Panel 3 was inoculated with either *F. graminearum* or *F. culmorum*. The assessment of open flowering score and AR displayed a continuous variation from dominating chasmogamy to complete cleistogamy. Significant differences for deoxynivalenol and T-2 were found, with a modest correlation between both mycotoxins. The lowest mycotoxin levels were found in two old and one modern cultivar, and the highest levels were found in a dwarf oat cultivar. Compared with plant height, AR was a rather ambiguous factor for the mycotoxin content, and it interfered with

Abbreviations: AE, anther extrusion; AR, anther retention; ARrel, percentage flowers with retained anthers; BBCH, plant growth stage; DON, deoxynivalenol; FHB, Fusarium head blight; FIK, *Fusarium*-infected kernels; GC, germination capacity; HULL, hull percentage; LOH, lodging prior to harvest; OFL, open flowering; PH, plant height; QTL, quantitative trait locus.

effects of other traits displaying high ranges such as earliness, lodging, or hull content. To unravel components of resistance to *Fusarium* in oats more precisely, specific populations with lower ranges in plant height and heading date should be studied.

1 | INTRODUCTION

Epidemic incidences of Fusarium head blight (FHB) in small-grain cereals are favored by warm and humid weather and abundant inoculum sources from cereal crop residues due to reduced tillage systems and high portions of cereals or maize (*Zea mays* L.) in the rotation (Wegulo, Baenziger, Nopsa, Bockus, & Heather, 2015). In oats (*Avena sativa* L.), FHB has been found to be a problem of increasing importance in the Nordic countries over last 30 yr. The most important *Fusarium* species in oats in Northern Europe are *F. graminearum* Schwabe*., F. poae* (Peck) Wollenw., *F. langsethiae* Torp & Nirenberg*, F. avenaceum* (Fr.) Sacc.*, F. sporotrichioides* Sherb., and *F. culmorum* (W. G. Sm.) Sacc. (Georgieva et al., 2018; Hietaniemi et al., 2016; Hofgaard et al., 2016; Yli-Mattila, 2010). Besides losses in seed quality due to infection (Bjørnstad & Skinnnes, 2008; Tekle, Skinnes, & Bjornstad, 2013), the accumulation of mycotoxins, such as deoxynivalenol (DON), T-2 and HT-2 toxin is the major concern in oat production.

Several breeding programs and research projects are ongoing to solve or reduce the threat of mycotoxin contamination in oats. Although most oats are generally considered to be susceptible to *Fusarium*, some less susceptible cultivars have been identified (Bjørnstad et al., 2017; Tekle et al., 2018; Yan et al., 2010). *Fusarium* resistance in oats, like in most cereals (Buerstmayr, Ban, & Anderson, 2009; He, Skinnes, Oliver, Jackson, & Bjørnstad, 2013), has been shown to be quantitative and based on minor as well as major genes. Based on findings in wheat (*Triticum aestivum* L.), Mesterhazy, Bartok, Mirocha, and Komoroczy (1999) suggested a system to classify *Fusarium* resistance into five types: (I) resistance to initial infection (Schroeder & Christensen, 1963), (II) resistance to the spread of infection (Schroeder & Christensen, 1963), (III) resistance to toxin accumulation (Miller, Young, & Sampson, 1985), (IV) resistance to kernel infection (Mesterhazy et al., 1999), and (V) tolerance (Mesterhazy et al., 1999). In addition to these components, there are several avoidance mechanisms that are linked to morphological or agronomical traits such as height and earliness (Mesterhazy et al., 1999). For oat with long distances between individual spikelets within a panicle, an inherent Type II resistance was stated (Langevin, Eudes, & Comeau, 2004; Tekle, Dill-Macky, Skinnes, Tronsmo, & Bjornstad, 2012). Therefore, resistance to infection (Type I) could be more important in oat breeding, and this assumption foregrounds the importance of studying the relationship between flowering traits and resistance to *Fusarium* in oats.

As in other cereals, oats are most susceptible to *Fusarium* infection during the flowering stage (Parry, Jenkinson, & McLeod, 1995; Tekle et al., 2012; Xue et al., 2015). Oat flowering is affected by fluctuations in temperature (Fruwirth, 1905; Misonoo, 1936). Humid and warm weather promotes open flowering (OFL; Callaghan, 1931), but it also promotes *Fusarium* infections (Hjelkrem et al., 2017). This interacts with less protected tissues of young palea, lemma, and stigma of open flowers and the amount of decaying anthers and pollen between the glumes, serving as a mycelium-growth-supporting medium (Kang & Buchenauer, 2000; Strange & Smith, 1971). The relevance of anther extrusion (AE) or anther retention (AR) for infection with *Fusarium* has been described in wheat (Buerstmayr & Buerstmayr, 2015, 2016; Gilsinger, Kong, Shen, & Ohm, 2005; Graham & Browne, 2009; He et al., 2016; Kubo et al., 2010, 2013; Skinnes, Semagn, Tarkegne, Marøy, & Bjørnstad, 2010; Steiner et al., 2019; Strange & Smith, 1971) and in barley (*Hordeum vulgare* L.; Yoshida, Kawada, & Nakajima, 2007; Yoshida, Kawada, & Tohnooka, 2005). For both cereals, it was found that infestation was slower when anthers or pollen were not available for *Fusarium* species. Therefore, either plants with very high AE (anthers are lost by wind) or cleistogamous plants displayed lower rates of infestation. Infection studies with limited oat genotypes indicate similar effects of AE or the presence of pollen on *Fusarium* infection in oats as in wheat (Divon, Bøe, Tveit, & Klemsdal, 2019; Tekle et al., 2012). However, studies confirming this hypothesis with more oat genotypes are missing.

Flowering in oats takes longer than in wheat or barley, and it usually occurs in the afternoon (Callaghan, 1931; Misonoo, 1936), although it can be delayed or accelerated by environmental conditions. A small drop of 0.5–2 °C within an hour from the highest temperature of the day promoted OFL in most of the studied *Avena* species (Nishiyama, 1970). According to Misonoo (1936), average flowering time of an oat panicle is 7–10 d. Since the main panicle starts flowering before the panicles of the side tillers, flowering can last >2 wk depending on the number of tillers. The uppermost flowers develop first within a panicle, and each flower stays open approximately 1.5–3 h d^{-1} during flowering. Because flowering intensity and duration are highly dependent on time and weather, OFL scores are rather snapshots of a dynamic trait.

In addition to flower opening, AE can be scored or recorded by counting the number of anthers retained inside the flower. This gives an indirect quantitative measure for the degree of flower opening. As shown by Heslop-Harrison and Heslop-Harrison (1996), flower opening as seen by swelling lodiculi and AE due to elongation of filaments are correlated events, except if flower opening is impeded by any morphological or physiological reasons or an environmental effect. In this study, the genetic variability of flowering parameters in three different oat panels was evaluated in contrasting environments. For two of the three independent experiments, the relation of flowering traits to *Fusarium* toxin accumulation was analyzed to reveal if flowering traits are exploitable targets for improving resistance to *Fusarium*.

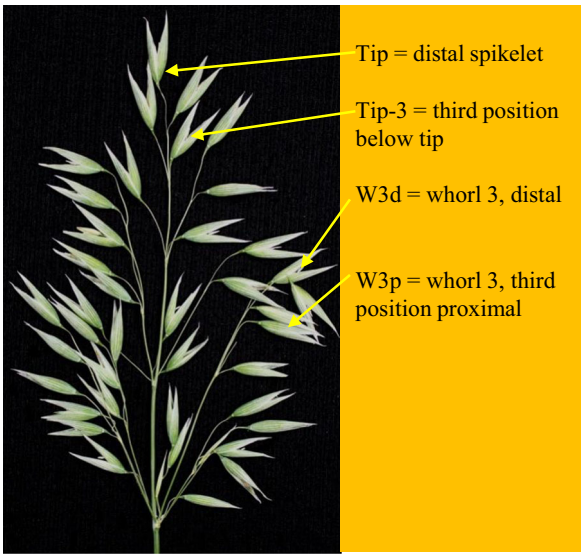

FIGURE 1 Spikelet positions within an oat panicle chosen for anther counts

2 | MATERIAL AND METHODS

2.1 | Experiments

Experiments were carried out in field trials at three different locations in Germany and Finland. The first experiment aimed to identify cleistogamic oats. Therefore, based on preliminary observations, an oat panel (Panel 1) consisting of 50 genotypes was compiled and evaluated in 2016 at three climatically different sites: Freising (southern Germany; 48°24′03″ N, 11°44′38″ E; 453 m asl; fluvic gleyic phaeozem), Groß Lüsewitz (northern Germany; 54°04′15″ N, 12°19′18″ E; 37 m asl; sandy loam), and Laukaa (Finland; 62°19′22″ N, 25°59′05″ E; 100 m asl; silt clay). The experiments were set up in a randomized block design with two replications at each site, two rows per plot, and 30 seeds per row with 20-cm distance between rows. In Finland, the plots were treated with sulfonylurea herbicide (15 g ha^{-1} CDQ SX, Dupont). The plant growth stage (BBCH) was recorded according to the extended BBCH scale by Hack et al. (1992). Anther extrusion was scored after the end of flowering, ~2 wk after the flowering started. Eight panicles per plot were bagged with two transparent bags (Crispac, Baumann Saatzuchtbedarf) to prevent anthers being blown away by wind. The amount of extruded anthers was estimated using a scale from 1 (no anthers visible) to 9 (100% of spikelets anthers pushed out or collected in the bag).

Anther retention was determined by opening the spikelet's primary floret and counting the anthers retained in four defined panicle locations (Figure 1) for 10 panicles per plot, frozen when flowering was finished.

Open flowering was scored two to three times during the flowering period by estimating the percentage of open flowers, at first within the upper half of the panicle and then 2–4 d later, within the lower half of the panicle. Mean values over both positions and scoring dates were used for statistical analysis. Differences in opening angle were not considered.

For the second experiment, a panel (Panel 2) consisting of 17 mainly modern oat cultivars and eight accessions was selected. According to previous tests, the accessions display a high OFL level and medium to high *Fusarium* resistance. Oats were seeded at three sites—Göttingen (51°36′ N, 9°55′ E; soil type loamy limestone on shell-limestone), Böhnshausen (51°51′ N, 10°57′ E; 146 m asl; sandy loam texture), and Groß Lüsewitz—in 2016 and 2017. Since AR was assessed in 2016 at all three sites and in 2017 only from Groß Lüsewitz, we analyzed the whole dataset only for these four environments. Oats were inoculated in blocks with five different treatments: (a) *F. langsethiae*, (b) *F. sporotrichoides*, (c) mixture of *F. sporotrichioides* and *F. culmorum*, (d) *F. culmorum*, and (e) water. Each treatment was set up as a randomized block design with three replications per entry, randomized within two groups of similar heading date and plant height (PH) to lower neighborhood effects in the second year. The distances between blocks of treatments were at least 9 m in 2017 in Groß Lüsewitz and longer (up to 300 m) in the other environments. Plots had a 1.5-m width and 1.2-m length (1.8 m^2) in Groß Lüsewitz with a seeding density of 300 seeds m^{-2}. In Göttingen and Böhnshausen, the plots had a size of 2 m^2. Herbicides, fertilization, and field management were conducted according to local agricultural practice and according to the needs considering the strong lodging tendency of the eight unadapted genotypes. There was no application of growth regulators or fungicides in Groß Lüsewitz.

Oats were inoculated using spore suspensions of the respective *Fusarium* species with 1×10^6 spores ml^{-1} for *F. langsethiae*, 5×10^5 spores ml^{-1} for *F. sporotrichioides* and *F. culmorum*, and 2.5×10^5 spores ml^{-1} of *F. sporotrichioides* as well as *F. culmorum* for the mixture. For each species, at

least two isolates showing high toxin production were used to produce the inoculum. Inoculations were performed with motor-driven backpack sprayers two times during flowering, considering different flowering dates of the panel. Before and after inoculation, the plots were irrigated in Groß Lüsewitz in 2016 and 2017. Alongside BBCH (see first experiment), PH was measured in centimeters from the soil surface to the tip of the panicles of the plot. Lodging prior to harvest (LOH) was scored using a scale from 1 (no lodging) to 9 (total lodging) at full ripening. Plots were harvested manually with 80–200 panicles per plot. After threshing, each grain sample was thoroughly mixed, and randomly taken subsamples of 30–50 g were ground using a centrifugal mill, the mesh size of the sieve being 1 mm (ZM 200, Retsch) for mycotoxin measurements. Mycotoxins DON and T-2 were measured by a serological assay (ELISA RIDASCREEN Kit R5906 and R3805, R-Biopharm) according to the manual. Single data matching the lower limits of detection (LoD) for DON (150 µg kg^{-1}) and T-2 (49 µg kg^{-1}) were set to LoD/2 for statistical analysis. A second grain sample of 50 g was dehulled with a laboratory impact dehuller (Friedrich Falke Maschinenbau, Mühlenbau), and the hull percentage (HULL) was calculated. For determining AR in Panel 2, the same method as for Panel 1 was applied, with 10 panicles per plot from water treatments in four different environments. Additionally, for comparisons with the wheat studies of Steiner et al. (2019), we deduced the percentage of AR as a percentage of flowers with retained anthers (ARrel) based on counting data, transforming single counting data into anthers or no anthers within a flower. This ARrel was based on the assumption that for successful *Fusarium* infection, it might be important that there is at least one anther retained between the glumes, and if more anthers are retained, it does not lead to more severe infection.

For the third experiment, a panel (Panel 3) consisting of 16 genotypes from Panel 1 and Panel 2, respectively, with a maximum range of cleistogamous and chasmogamous flowering was selected. This experiment was performed in Groß Lüsewitz and in Laukaa in 2017. The experimental design was a randomized block design with two replications of two-row plots. In Laukaa, the herbicide Ariane S (2.0 L ha^{-1}, Dow Agro Sciences) and the insecticide Fastac 50 EC (0.2 L ha^{-1}, Bayer Crop Science) was applied prior heading. Infected oat kernels, colonized with a mixture of five Finnish *F. graminearum* isolates (05011, 12008, 06249, 05039, and 12010), served as inoculum of oats in Laukaa. Inoculum was evenly distributed (10 g m^{-2}) in the field at BBCH Growth Stage 32. The inoculated field was mist irrigated daily for 10 min every hour between 7:00 and 10:00 p.m. until yellow maturity. In Groß Lüsewitz, inoculation was performed twice during flowering with a spore suspension of *F. culmorum* (5×10^5 spores ml^{-1}) as described above for the Panel 2. All plots were hand harvested when the plants reached maturity or when the growing season ended, as was the case for some late-ripening varieties in 2017. In Laukaa, harvested panicles were dried with a warm-air dryer directly after harvesting. From all grain samples, the incidence of *Fusarium*-infected kernels (FIK, %) was determined. Therefore, 50 randomly selected grains from each plot were placed in petri dishes containing selective pentachloronitrobenzene (PCBN) medium (Nash and Snyder medium; Nelson, Toussoun, & Marasas, 1983). The FIK was assessed at 2 and 7 d after incubation at 23 °C. Because of weak differentiation after 1 wk, only results at 2-d incubation time are outlined below. Pure fungal cultures were obtained from hyphal tips of the isolates grown out from grains harvested from the experimental site in both years in Finland and incubated on potato dextrose agar medium. These isolates were identified based on their spore morphology under the microscope in order to ensure that the plants were infected with the desired *Fusarium* species. For germination capacity (GC, %) a standard paper test from a sample of 100 grains per replicate was performed (ISTA, 2006). The DON content was measured using a serological assay (ELISA RIDASCREEN Kits R5906 and R3805, R-Biopharm) according to the manual.

2.2 | Statistical analysis

To homogenize error variances, trait data in percentage (OFL, HULL, and GC) were transformed according to the logit function $L = \ln(p)/(1 - p)$, and toxin data were log transformed. The AR, AE, PH, BBCH, and LOH data were transformed using the Box–Cox transformation (Box & Cox, 1964). Basic statistical parameters like skewness and kurtosis, as well as variances (ANOVA), were calculated with PLABSTAT version 3A (Utz, 2011). In the ANOVA models, each year–site combination was considered as a single environment, and genotypes, environments, and replications were defined as random. Broad-sense heritabilities were calculated according to Knapp and Bridges (1987). Because of nearly identical heritability values between lme runs in R and the output of PLABSTAT, only results based on the latter software are presented.

For multiple comparisons of means, Tukey's honestly significant difference (HSD) (Steel, Torrie, & Dicky, 1997) and LSD tests were applied. Plots were drawn using the R package ggplot2 (Wickham, 2016).

3 | RESULTS

The evaluation of flowering traits in Panel 1 revealed significant differences in OFL levels and AE (Table 1, Supplemental Table S1). Despite environment and genotype × environment interaction effects, the ranking was not severely impaired by

TABLE 1 Minimum, maximum, mean, genotypic variance (σ^2_G), genotype × environment interaction variance (σ^2_{GxE}), and heritability (H^2) for anther extrusion (AE), development stage (BBCH), and open flowering score (OFL) of oat Panel 1 (50 entries, three sites)

Statistic	OFL	AE	BBCH
	%		
Min.	0.00	1.00	40.00
Max.	80.00	8.00	70.50
Mean	24.25	2.77	53.83
σ^2_G	0.59**	0.15**	8.24**
σ^2_{GxE}	0.20**	0.11**	13.71**
H^2	76.22	66.95	64.83

Note. Variances and heritabilities are based on transformed data for OFL and AE, respectively.
**Significant at the .01 probability level.

environments, shown by relatively high heritabilities for OFL, AE, and BBCH of 76, 67, and 65%, respectively.

There was a continuous gradient from predominant chasmogamy in Simon and Vista, with ∼50% open flowers, to nearly complete cleistogamy in Aveia and Pony based on AE as well as OFL score (Supplemental Table S1). Between OFL and AE, the phenotypic correlation in Panel 1 was highly significant with $r = .6$, irrespective of a few different AE scores in entries with equal OFL level. For 10 genotypes in Panel 1, the AR was assessed additionally, confirming cleistogamy for Aveia and Pony with almost maximal AR values (both cv. AR = 2.93). Within this subpanel, coefficients of correlation between AE and AR were $r = -.94$ and $r = -.85$ between OFL and AR.

Panel 2 with 25 genotypes was grown at three sites in 2016 and 2017. Below, we will focus on AR and its relation to DON and T-2 mycotoxin content. In addition, subsets of environments were also applied to data for PH, BBCH, LOH, and HULL, to study their correlation to mycotoxin accumulation.

Analyses of variance for Panel 2 displayed significant effects of genotype, environment, and their interactions on all assessed traits (Supplemental Table S2). The heritabilities for all five traits were comparably high (Supplemental Table S2). The genotypes displayed wide ranges for most traits (i.e., the dwarf phenotype of the cultivar Troll was 40–50 cm shorter than the older accessions, which showed a high tendency to lodging, higher hull content, and late and more OFL). For AR, Zorro displayed the highest reading with 2.6 anthers per flower retained, and AVE1284 displayed the lowest with 0.8 anthers per flower. Thus, there was no absolute chasmogamic or cleistogamic genotype among the tested oats in Panel 2. The highest levels of *Fusarium* toxins were found in cultivars Troll and Bessin, and the lowest toxin levels were found in Puhti and Schenkenfeldener (Table 2). The BBCH, scored in Groß Lüsewitz only, was significantly correlated to DON ($r = .45$) and T-2 ($r = .7$), indicating higher toxin levels for the early-flowering genotypes.

The correlations between PH and mycotoxin levels ($r = -.67$ for DON and $r = -.84$ for T-2) were significant, and it was informative to evaluate how a high range in PH influenced the correlations between toxins and AR. Therefore, in Table 3, the r_{phen} and r_{gen} are displayed based on all entries with a high range in PH, and additionally on a subset of 16 entries with similar PH, without Troll and the elder accessions.

The relation between both mycotoxins and lodging was negative for both datasets, reflecting lower mycotoxin levels in entries like Schenkenfeldener or Keely with higher lodging, and higher mycotoxin levels in cultivars with better lodging resistance like Bison. Between mycotoxin levels and HULL readings, only weak and nonsignificant correlations were found. Comparing r_{gen} among AR, ARrel, and DON or T-2 based on 25 entries, positive correlations (r_{gen} and r_{phen}) were found, indicating that high AR values entail higher toxin values. When correlations were calculated only with the subset of 16 oats of similar PH, correlation coefficients turned out to be negative. The strong influence of few entries with contrasting PH on the correlation indicated a weak or nonlinear relationship between toxin accumulation and AR. To further assess the relationship between AR and mycotoxins, scatterplots of AR as well as ARrel and DON and T-2 (Figure 2), respectively, were drafted by using mean data over replications and experiments. In the four scatterplots in Figure 2, oat genotypes are colored according to PH. The tall entries (light blue dots) comprising the elder genotypes, showing lower AR and ARrel, whereas the medium-high entries represent modern genotypes, with some higher AR and ARrel and some higher DON, as well as T-2, values compared with tall oats. The scatter of dots show high toxin values only in combination with medium AR from 1.5 to 2.5 and ARrel of 70–95%. However, low mycotoxin contents are present in medium levels of AR and ARrel, as well as in the lowest and highest AR values.

Results of Panel 2 showed a medium range in AR and rather ambiguous relationships between AR and mycotoxin levels. Panel 3 consisted of genotypes ranging from cleistogamic to chasmogamic flowering to study the cause relationships between mycotoxin accumulation and flowering performance. We recorded BBCH, PH, OFL, and AR as in Panel 1, and additionally the FIK (%), GC (%), and DON accumulation (μg kg^{-1}) (Table 4). Deoxynivalenol readings were found in very high ranges with many outliers for most of the genotypes, which was not solved by transformation. Therefore, we displayed only the medians for DON, which were less influenced by outliers compared with arithmetic means. Data of Panel 3 confirmed cleistogamic flowering of cultivars Aveia and Pony, first detected in Panel 1 experiments, and the greater OFL of cultivars Waterloo, Schenkenfeldener, and Puhti, involved in Panel 2 as well. This was in line with

TABLE 2 Mean anther retention (AR) at four environments, back-transformed deoxynivalenol (DON) and back-transformed T-2 in oat grains, plant height (PH), lodging prior to harvest (LOH), development stage (BBCH), and hull percentage (HULL) of 25 genotypes

Entry	AR	DON	T-2	PH	LOH	BBCH	HULL
		μg kg^{-1}		cm	1–9[a]		%
LSD	0.29	SG	SG	4.3	1.6	1.4	2.3
Modern cultivars							
Troll	2.47	4,945.7a	231.9a	80.1	2.8	51.2	33.2
Zorro	2.60	1,902.1cdef	66.0cdefgh	95.0	4.6	51.5	32.2
Tim	2.11	2,138.9cdef	60.1defgh	95.7	3.8	54.0	28.2
Bessin	1.82	4,523.4ab	128.4ab	96.5	4.4	51.9	31.4
Max	2.24	2,465.9bcde	106.1bcde	97.9	4.3	52.4	29.0
Simon	2.11	2,086.3cdef	56.9efgh	98.1	4.3	53.2	31.0
Husky	2.08	1,593.4defgh	92.3bcdef	99.3	3.7	54.0	31.0
Bison	1.90	2,382.8bcde	101.5bcde	99.5	2.3	54.8	30.1
Typhon	2.19	2,395.0bcde	113.0bcd	99.8	4.3	53.1	31.4
Canyon	2.22	1,996.4cdef	96.9bcdef	101.5	3.9	53.6	30.7
Harmony	2.03	2,023.5cdef	109.9bcd	102.4	3.2	53.0	30.3
Scorpion	2.25	3,426.6abc	87.6bcdef	102.6	4.1	52.1	30.9
Poseidon	2.07	30,76.6abcd	113.7bcd	102.6	3.9	51.8	31.2
Yukon	2.18	1,912.3cdef	116.3bc	103.2	3.2	51.9	31.2
Keely	2.19	1,473.2efgh	67.4bcdefg	104.8	4.4	52.3	32.9
Apollon	1.83	2,306.4cde	93.0bcdef	105.7	3.4	53.0	30.1
Symphony	2.06	1,359.5efgh	56.5efgh	110.4	3.4	50.7	29.7
Elder cultivars or accessions							
AVE 1490	1.39	1,408.1efgh	51.3fgh	115.5	8.3	48.3	33.6
Waterloo	1.00	1,719.4defg	39.1gh	120.8	7.8	45.0	33.9
Puhti	2.08	930.4gh	35.3gh	124.2	3.9	48.3	34.3
AVE 1284	0.80	1,482.5efgh	39.4gh	124.6	6.9	43.4	35.1
Schenkenfeldener	1.17	861.1h	35.0h	125.0	8.3	47.3	32.5
Buki tf.	1.28	2,070.1cdef	39.4gh	129.3	7.2	43.2	32.0
Zlat Kisa	1.61	1,593.1defgh	39.2gh	129.3	6.3	43.5	32.5
Lovaszpatoi sarga	1.25	1,105.9fgh	37.1gh	132.8	6.1	43.3	32.6

Note. Means in rows not sharing a common letter (significance groups = SG) significantly differ according to Tukey's honestly significant difference test ($P < .05$). Least significant differences (LSD, $p = .05$) between genotypes are reported for AR, PH, LOH, BBCH, and HULL. Genotypes are sorted by PH.

[a]1 = no lodging, 9 = total lodging.

similar results for PH and heading of most cultivars in all the experiments.

Based on the rankings of DON levels, AR, and OFL, the most cleistogamous (Aveia) and most OFL types (Schenkenfeldener, Waterloo, AVE1490, and Nora) were those with low to modest DON medians (Table 4). The low DON level in Aveia may be related to its PH, which is otherwise similar to PH of cultivars Pal, Jaak, Waterloo, and others with higher DON medians. The varieties Pony and Nora showed the lowest PH in Panel 3. Interestingly, DON medians in both cultivars were medium to low, which may be related to the high level of cleistogamy of Pony and rather chasmogamous flowering of Nora, which may have hampered DON accumulation.

Similar to Panel 2 there were low DON readings over the whole range of OFL and AR, and higher DON readings combined with medium AR values in Panel 3. There was no significant correlation between DON levels and AR or OFL or GC (Supplemental Table S3), but significant correlations between DON levels and PH ($r_{phen} = -.62$, $p = .05$), FIK ($r_{phen} = .69$, $p = .01$), and BBCH ($r_{phen} = .53$, $p = .01$), and between AR and OFL ($r_{phen} = -.85$, $p = .01$).

4 | DISCUSSION

4.1 | Genetic variability of flowering traits

In this study, a high level of genetic variability of flowering traits in oats, varying from full cleistogamy to a high level of chasmogamy, is described. Completely cleistogamic

TABLE 3 Phenotypic and genotypic coefficients of correlation in Panel 2 (r_{phen} above the diagonal and r_{gen} below the diagonal) between traits, deoxynivalenol (DON, natural log-transformed, μg kg^{-1}) and T-2 (natural log-transformed, μg kg^{-1}), anther retention (AR), anther retention percentage (ARrel), hull percentage (HULL), and lodging prior to harvest (LOH), based on 25 cultivars (above) and 16 cultivars of similar height (below)

Parameter	T-2	DON	AR	ARrel	HULL	LOH
25 entries						
T-2		.86**	.54**	.59**	−.35	−.68**
DON	1.00++†		.48*	.49*	−.35	−.66**
AR	.64++	.58++		.97**	−.53**	−.74**
ARrel	.76++	.60++	.99++		−.64**	−.80**
HULL	−.43+	−.36+	−.60++	−.71++		.77**
LOH	−.85++	−.79++	−.78++	−.83++	.83++	
16 entries with similar plant height						
T-2		.60*	−.27	−.11	.23	−.25
DON	.85+		−.44	−.45	.12	−.35
AR	−.77+	−.62++		.92**	.42	.59*
ARrel	−.23	−.58++	.97++		.30	.55*
HULL	.28	.10	.45+	.35+		.42
LOH	−1.00	−.70+	.70++	.71++	.51+	

*,** Significant at the .05 and .01 probability levels, respectively.
†+ or ++ r_{gen} is greater than the single or doubled standard error, respectively.

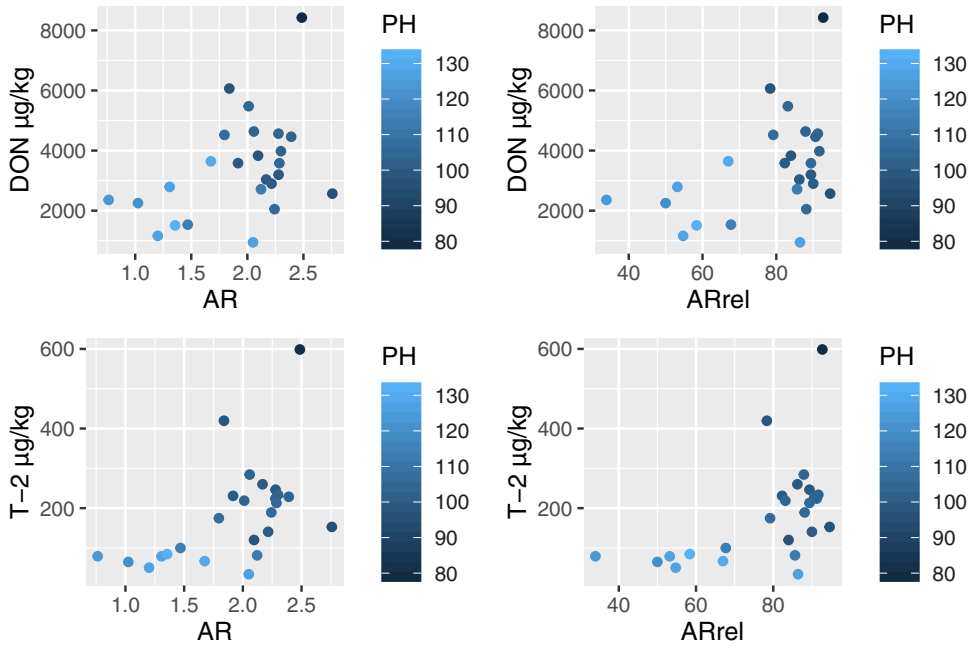

FIGURE 2 Scatterplots of anther retention (AR) vs. deoxynivalenol (DON) and percentage flowers with retained anthers (ARrel) vs. DON (upper two plots) and AR vs. T-2 and ARrel vs. T-2, respectively. Coloring is related to plant height (PH). Each dot represents the mean over three replications and four environments of 25 genotypes of Panel 2

flowering found in cv. Aveia was easy to assess compared with higher levels of chasmogamy, which entailed some unavoidable inaccuracies when assessing AE and OFL. Scoring of OFL is almost a snapshot of a dynamic trait, because of the short and changing daytime frame of flower opening influenced by weather conditions. We repeated OFL scoring during the flowering period to increase precision and found relatively high heritabilities in both tested oat panels (Panel 1 and Panel 3). However, scoring of OFL in larger panels is challenging because of the uncertain differentiation

TABLE 4 Mean anther retention (AR), open flowering (OFL), plant height (PH), DON (median), BBCH, *Fusarium*-infected kernels (FIK), and germination capacity (GC) of the 16 entries of Panel 3 based on experiments in Groß Lüsewitz and Laukaa in 2017, and heritability (H^2), based on transformed data (sorted for DON median)

Entry	AR	OFL	PH	DON	BBCH	FIK	GC
			cm	µg kg^{-1}		%	
H^2	91.70	76.7	89.0	–	–	50.3	53.3
Aveia	2.86	1.3	111.8	863	51.9	6.3	63.3
Schenkenfeldener	1.27	42.2	126.3	1,686	55.6	6.8	89.8
AVE 1490	1.86	33.3	111.8	1,959	54.1	6.8	77.0
Waterloo	1.36	53.4	119.0	2,165	52.0	6.0	81.5
Vista	2.31	35.9	108.0	3,294	56.5	6.0	82.0
Symphony	2.02	40.5	107.8	3,944	58.0	7.0	84.0
Pal	2.30	32.5	114.8	4,316	57.0	8.3	84.3
Puhti	1.87	43.4	117.3	4,629	56.0	5.8	74.3
Nora	1.66	41.6	95.8	4,722	55.0	6.5	75.5
Chaps	1.68	39.1	101.3	4,722	53.2	8.5	68.8
Jaak	2.01	39.1	112.0	5,653	58.0	16.3	73.0
Longchamp	2.52	23.9	101.8	5,884	53.1	14.0	75.3
Pony	2.98	8.4	95.3	6,374	54.0	12.3	73.8
Simon	2.29	43.2	99.4	7,259	57.4	8.4	82.1
Iltis	2.35	35.6	103.8	7,406	58.0	13.8	79.0
Tim	2.21	35.6	100.0	10,301	59.8	20.0	57.3

between cleistogamous panicles and those that did not yet start flowering. Anther retention, based on counting the number of retained anthers, is a quite precise quantifiable trait. In the case of cleistogamy, all anthers remained within the flower and AR reached the maximum number of 3. However, there seemed to be a limit to quantify strong chasmogamy, because a few anthers might have been stuck within the flower although it was fully opened. Therefore, full chasmogamy with AR = 0 and OFL = 100% are maximum values, which were not achieved by the oats tested. Furthermore, scoring AE is quite a rough estimation of true AE because AE does not take into consideration the number of anthers remaining within the flowers. Another approach would be necessary to assess the level of OFL more precisely.

The significant coefficients of correlation between OFL and AR, with $r = -.85$ for Panel 1 as well as for Panel 3, are based on similar physiological processes of flower opening or lodiculae swelling and filament elongation (Heslop-Harrison & Heslop-Harrison, 1996).

Stråbø (2015) found similar ranges for AE in older oats of Scandinavian origin, with low AE in modern genotypes like Typhon. The AE in cultivars Norum and Stormogul (Stråbø, 2015) was similar to that of the most chasmogamous genotypes like AVE1284 or Schenkenfeldener of Panel 2 and Panel 3 used in this study. Schenkenfeldener, a rather old variety, was already described by Zechner (2002) as a more open-flowering type, which was confirmed in this study. Interestingly, a high level of OFL was also found in modern oats like Simon, indicating a low selection pressure for more closed flowering types, associated with lower outcrossing tendency and lesser infection potential with smut [*Ustilago avenae* (Pers.) Rostr.]. It seems, however, that selfing is sufficiently retained even for the most open-flowering accessions.

Considering the high heritability of AR and OFL, and possible transgressions in both directions for AE (Stråbø, 2015), selection for a more favorable flowering character in oats could be effective.

4.2 | Flowering traits and *Fusarium* avoidance

There are several studies demonstrating that the infection of cereal flowers by *Fusarium* is expedited by pollen and anthers sticking between hulls. When anthers and pollen are not accessible for the pathogen due to male sterility, emasculation, chasmogamy, or cleistogamy, infection proceeds slower, which also depends on environmental conditions and resistance of the plant. In studies by Buerstmayr and Buerstmayr (2016), He et al. (2016), and Steiner et al. (2019), an increased AR was correlated with higher FHB severity, whereas in studies by Dickson, Johann, and Wineland (1921), Skinnes et al. (2010), or Kubo et al. (2013) wheat lines with the lowest as well as the highest AE displayed the lowest FHB levels.

Since decaying pollen and anthers are substantial sources of pathogen growth and assuming the lowest availability of anthers and pollen for cleistogamous (AR = 3) and

chasmogamous (AR = 0) flowering, we expected an inverse parabolic dependency between AR and toxins. Interestingly, we found many genotypes with intermediate AR but very low mycotoxin levels, which indicates that AR is neither the only factor, nor the factor with greatest impact on mycotoxin accumulation. Plant height and related traits affected mycotoxin accumulation in Panel 2 and Panel 3, as found in other studies as well. For instance, the dwarf cultivar Troll is carrying the *Dw6* gene, which is possibly pleiotropically linked to *Fusarium* susceptibility in oats, according to a quantitative trait locus (QTL) study with another *Dw6*-carrier cv. Buffalo (Stancic, 2016). In contrast with Troll or Pony, the elder cultivars or genebank accessions were about 20 cm taller with wider panicles than the modern genotypes, showed late and more OFL, had a high tendency towards lodging, and contained high portions of hulls. Lodging and a high hull content usually increase mycotoxin accumulation, because most mycotoxins accumulate in the hulls. Escape effects caused by wide panicles, late flowering, and increased PH cannot be ruled out in our experiments. It was impossible to disassemble these factors via a mixed-model approach (Emrich, Wilde, Miedaner, & Piepho, 2008) because of the unbalanced data recording at the different sites. In addition, there were probably more factors contributing to mycotoxin accumulation in oats.

The variation in the amount of pollen and in its deposition site in the inner surface of palea and lemma could cause variation in *Fusarium* infestation and in mycotoxin accumulation. Even in wide opened flowers with extruded anthers, the author observed high amounts of pollen on the inner side of lemma, probably due to anthers dehiscence within the flower before opening. Fruhwirth (1905) observed that frequently two anthers are trapped by the folds of the palea, corresponding to the AR mean of 1.9 and 2.1 for Panel 2 and Panel 3, respectively. Pollen deposition and AR within the flower were possibly promoted by a more upwards-oriented flower, as observed in the variety Pony. However, this orientation was rare in recently bred oats. Of more importance were differences in mycotoxin content between genotypes like Tim (low DON content) and Bessin (high DON content) or Keely (low DON content) and Scorpion (high DON content) with similar PH, AR, and BBCH in Panel 2. Possible reasons for such differences were detoxification of DON (Michlmayr et al., 2018) or a variation in trichome-type cells, which were found to be related to *Fusarium* ingress and resistance responses in barley (Imboden, Afton, & Trail, 2018).

In our experiments with Panel 3, we focused on DON, FIK, and GC as resistance criteria. According to Tekle et al. (2018), the correlation between GC and DON was low when DON contamination ranged from 0 to 5 mg kg^{-1}, as it was roughly the range in Panel 3 of this study. In Panel 3, the correlation seemed mainly to be impaired by low GC in Aveia, which was the most cleistogamic cultivar in this study.

The results of this study support findings by Bjørnstad et al. (2017), Gagkaeva, Gavrilova, Orina, Blinova, and Loskutov (2017), and Tekle et al. (2018) that cv. Bessin in Panel 2 is highly susceptible to *Fusarium*, leading to high mycotoxin accumulation in the grains. In contrast with Bessin, cv. Symphony showed low mycotoxin levels in our experiments but higher susceptibility in the Norwegian study (Tekle et al., 2018). These contradicting results may be caused by different inoculation methods applied and genotype × environmental interactions.

Since oats are most susceptible to *Fusarium* infection during flowering (Tekle et al., 2012; Xue et al., 2015), and also because of the colocation of QTLs for AR and FHB in wheat (Steiner et al., 2019), a significant effect of AR on mycotoxin accumulation in oats was hypothesized. Results of Panel 2 and Panel 3 displayed that complete cleistogamy, as found in cultivar Aveia, or a high level of chasmogamy, such as in Schenkenfeldener, resulted in lower infection levels and mycotoxin accumulation, but there are several known and unknown factors interfering with AR and mycotoxin accumulation. A precise evaluation of the impact of AR on mycotoxin content will require tests in oat populations with less variation in PH and flowering date, but high variability in AR, as recently used in wheat (Steiner et al., 2019). Our results indicate that differences in AR in oats explained only a small part of genetic variability for resistance to *Fusarium*, and more research is needed to disassemble and depict the active and passive resistance components against *Fusarium* in this small-grain cereal.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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