Two oat genotypes with different field resistance to *Fusarium* head blight respond similarly to the infection at spikelet level

Juho Hautsalo¹ · Satu Latvala² · Outi Manninen³ · Minna Haapalainen⁴ · Asko Hannukkala^{2,4} · Marja Jalli²

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Abstract

Cultivar resistance is essential for the management of *Fusarium* head blight (FHB) disease in oat production. However, the breeders lack methods suitable for phenotyping disease resistance and resistance sources. In this paper we compared two oat genotypes, a rejected variety BOR31 and a landrace VIR7766, with four different traits that could reflect resistance to FHB in a greenhouse environment. Spray and point inoculations were used to inoculate *Fusarium graminearum* into flowering oat plants. When spray-inoculated, VIR7766 was significantly more resistant against the initial infection than BOR31, measured by the number of *Fusarium*-infected kernels and by DON accumulation. In the point-inoculated oats, the loss of fresh weight in the inoculated spikelet correlated well with the increasing *F. graminearum* biomass in the spikelet, measured six days after inoculation. However, no difference in the growth of the fungus was observed between the tested oat genotypes by point inoculation. We speculate that once the infection is established, the ability of the oat plant to resist the spread of the infection within a spikelet is low in the genotypes studied, although oat, in general, due to its panicle structure, is considered to have a high resistance against *Fusarium* infection.

Keywords Disease resistance · Panicle · Quantitative PCR · Resistance components · Screening methods

Oat (*Avena sativa* L.) has become increasingly popular for human consumption due to its health beneficial traits (EFSA 2009 and 2011). However, decreased seed quality due to *Fusarium* head blight (FHB) infections has led to rejections and market value reductions. Infection can reduce grain yield and especially its quality when mycotoxins accumulate in the grains, or germination capacity collapses (Bjørnstad and

Skinnes 2008; Tekle et al. 2013). The worst problems in oats are due to accumulation of mycotoxins, such as deoxynivalenol (DON), which inhibits protein synthesis and can cause symptoms both in humans and animals. Due to acute toxicity of DON, limits for its concentration in grain have been set by EU (European Commission 2006). *Fusarium graminearum* Schwabe is the most important DON producing species in the Nordic region (Hietaniemi et al. 2016; Hofgaard et al. 2016) and the most important causal agent of FHB worldwide (Trail 2009).

Management of FHB would benefit from resistant cultivars, since when severe disease incidence occurs, FHB cannot be fully controlled in oats by agricultural or manufacturing practises (Hietaniemi 2016). Less susceptible genotypes have been identified in recent research (Tekle et al. 2018, Bjørnstad et al. 2017, Gagkaeva et al. 2013), but the mechanisms behind the resistance are quantitative (He et al. 2013) and based on minor genes. Oat resistance against FHB is typically evaluated by measuring mycotoxin accumulation or other *Fusarium* associated traits such as infection rate or germination capacity from either greenhouse grown, spray-inoculated plants (Tekle et al. 2012; Xue et al. 2014) or from spawn-inoculated field nurseries (Gagkaeva et al. 2013; Tekle

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Asko Hannukkala is deceased on 10 May 2020.

✉ Juho Hautsalo
juho.hautsalo@luke.fi

¹ Natural Resources Institute Finland, Surfontie 9A, Jyväskylä FI-40500, Finland

² Natural Resources Institute Finland, Tietotie 4, Jokioinen FI-31600, Finland

³ Boreal Plant Breeding Ltd, Myllytie 10, Jokioinen FI-31600, Finland

⁴ Department of Agricultural Sciences, University of Helsinki, Helsinki FI-00014, Finland

et al. 2018). A third inoculation method, point inoculation, has been used for visual estimation of symptom spread in wheat (Zhu et al. 1999) and barley (Langevin et al. 2004), but this has not been shown to be valuable in oats, where the quantification of symptoms requires a strong control of environmental factors (Xue et al. 2014; Bjørnstad et al. 2017) and the symptoms are not found to spread across the panicle (Langevin et al. 2004) as they do in the spikes of wheat or barley.

The objective of this study was to use spray and point inoculation methods to investigate FHB resistance in two oat genotypes in a greenhouse. The number of *Fusarium*-infected kernels and DON accumulation were compared by spray inoculation experiments. Point inoculations were used to test whether it is possible to measure FHB resistance in oats by determining the *F. graminearum* biomass by real-time PCR or by measuring the damage as the loss of fresh weight shortly after anthesis.

Greenhouse-produced seed of a susceptible oat variety BOR31 (Boreal Plant Breeding Ltd., Finland) and a moderately resistant, brown-hulled, Chinese landrace VIR7766 [N.I. Vavilov All-Russian Institute of plant genetic resources (VIR), Russia] were sown in 2 litre pots containing fertilized peat (Kekkilä Taimimulta, Kekkilä Group, Finland) supplemented with sand, and fertilized weekly with liquid fertilizer (Yara Fericare, 14% N-11% P- 25% K- 2.4% MgO + micronutrients, Yara International, Norway). Plants were grown at 18 C/15 C (day/night). The light intensity was kept above 200 W/m² 16 h per day.

In a greenhouse, two separate spray inoculation and point inoculation experiments were conducted. Spray inoculation experiments had four pots with five plants per genotype and these were randomized within four replicates. The point inoculation experiments had five pots with one plant per pot. The plants were inoculated at anthesis (BBCH 65) with 200 ml of inoculum sprayed per 100 plants or 10 µl inserted within three spikelets per each plant (Fig. 1). The inoculum was prepared of the DON-producing *F. graminearum* isolate 05011, obtained from a cereal field in Finland in 2005 (Kokkonen et al. 2010). The inoculum concentration was 2.4×10^5 conidia/ml for the spray inoculation experiments and 0.5×10^5 conidia/ml for the point inoculation experiments. To obtain uniform dispersion of the conidia, Tween-80 (0.01%) was added to the point inoculation suspension. The control spikelets were “inoculated” with sterile water. For the spray-inoculated plants, mist irrigation was applied for 2 h before and from 6 h after inoculation for 14 h, whereas for point inoculations the panicles were covered with translucent plastic bags for 48 h following the inoculation. After both kinds of inoculations the temperature was raised to 20 C/18 C (day/night).

Main stems from each pot were harvested at BBCH 92 from the spray inoculated experiments (5 panicles per sample, 4 replicate samples per experiment). Ten grains from each

panicle were placed on selective pentachloronitrobenzene (PCNB) plates (Nash and Snyder medium, Nelson et al. 1983). *Fusarium*-infected kernels (FIK), showing bleaching and discolouration symptoms, were counted after one week incubation at 23 °C and shown as percentage of infected grains per replicate (n = 04 per genotype per experiment, 16 in total). DON contents were analysed from milled grain samples (n = 16) with ELISA kit (R5906 Ridascreen DON 96 test, R-Biopharm, Darmstadt, Germany). Hyphal tip cultures on PDA plates were made from the PCBN plates in each experiment and checked with microscope to confirm the causal agent of the infection.

At six days post inoculation (dpi), the point-inoculated spikelets were separately harvested and stored at -80 °C. A total of 60 inoculated spikelets (three technical repeats from five plants in two experiments and two genotypes) and 20 water-inoculated spikelets (one per plant) were weighed and analysed by real-time PCR for *F. graminearum* biomass (Supplementary material). The fresh weight reduction was determined by comparing the weight of each of the 30 *F. graminearum*-inoculated spikelets to the mean weight of the water-inoculated control spikelets

Fig. 1 In the point inoculations a droplet of *F. graminearum* inoculum was inserted between the palea and lemma of the primary oat floret. The outermost spikelets from the median part of the panicle were selected for the point inoculations

per experiment (10 in the 1st experiment and 30 in the 2nd experiment).

The landrace VIR7766 had significantly less infected kernels and DON accumulation than the rejected variety BOR31 (Table 1). This is in agreement with the two-year field resistance screenings (Gagkaeva et al. 2013) that rated the landrace, VIR7766, as a moderately resistant accession with multi-component resistance, resisting both mycotoxin formation and spreading of infection from hulls to the seed. In addition, BOR31 has been found to be very susceptible to DON accumulation and *Fusarium* infections in several greenhouse experiments made in Natural Resources Institute Finland, Luke (Hautsalo et al. 2020, submitted). ‘VIR7766’ has also brown hull which is a trait that has been associated with FHB resistance in oats (Rainio 1932, Loskutov et al. 2016), although the impact of this trait could not be evaluated in this study. In addition to that VIR accessions can have other interesting mechanisms that may restrict the infection such as the higher level of wax production in cv. Argamak (VIR14648) (Willforss et al. 2020).

Point inoculation of oat spikelets with the inoculum suspension resulted in accumulation of *F. graminearum* biomass within the spikelets (Fig. 2), which was measured at 6 dpi by real-time PCR (Supplementary material). Mixed model statistical analysis (SAS Enterprise Guide 7.1, SAS Institute Inc., Cary, NC, USA) was performed with the *F. graminearum*/plant DNA ratios normalized with log-transformation and genotype, experiments and their interaction set as fixed effect and replicates nested within experiments as random factors. The average *F. graminearum*/plant DNA ratio differed significantly ($p < 0.01$) between the first and the second point inoculation experiment, with mean $\pm$ S.D $92,500 \pm 153,000$ and 6700 ± 4500 , respectively. The oat genotypes did not differ in their relative *F. graminearum* biomass ($p = 0.50$). This was surprising, because several previous studies had shown that in *Fusarium*-infected oat the *Fusarium* DNA content and mycotoxin levels had a strong positive correlation in samples that were collected after ripening (Yli-Mattila et al. 2017; Gagkaeva et al. 2013; Fredlund et al. 2010) and the evidence suggested that ‘VIR7766’ could resist the spreading of infection into the grain (Gagkaeva et al. 2013). Moreover, in wheat and barley the resistant and susceptible genotypes can be

Fig. 2 Spikelet weight reduction showed statistically significant relation with the increase in *F. graminearum* biomass, determined six days after inoculation of the mid panicle region with *Fusarium graminearum* in two separate inoculation experiments. Results for the two different oat genotypes (VIR7766 and BOR31) in two different experiments (1st and 2nd) are represented by different point symbols

separated by *F. graminearum* biomass measurement after point inoculation by a similar method that was used in this study. The *F. graminearum* biomass results in wheat and barley correlated well with the visual estimations of spikelet and rachis resistance (Kumar et al. 2015; Kage et al. 2017). In a study on oats (Willforss et al. 2020), susceptible cv. Belinda and partially resistant cv. Argamak were compared for DON accumulation at panicle level. The difference in DON accumulation between these genotypes was not found significant at 4 dpi, although the difference was significant in the samples taken at harvest. Similar approach where *F. graminearum* biomass would be measured at harvest could supplement our study.

Based on the results of this study, we suggest that the difference in DON accumulation between ‘VIR7766’ and ‘BOR31’ may largely result from type I resistance, the resistance against initial infection (Schroeder and Christensen 1963). It seems that the mycotoxin accumulation in these oats is a result of a series of individual infections occurring simultaneously within the panicles, since on average the FIK and DON results support each other (Table 1). These results are

Table 1 The estimates for accumulation of DON mycotoxin and percentage of *Fusarium*-infected kernels and their standard errors from two separate spray inoculation greenhouse trials

Oat genotype	DON accumulation, $\mu\text{g/kg}$ ($\pm$ S.E.)	<i>Fusarium</i> -infected kernels, % ($\pm$ S.E.)
VIR7766	2735.8 ($\pm$ 178.6)	25.0 ($\pm$ 6.2)
BOR31	9966.2 ($\pm$ 178.6)	91.5 ($\pm$ 6.2)
Statistical analysis	$p < 0.05$, $\text{df} = 7$, $F = 6.55$	$p < 0.01$, $\text{df} = 7$, $F = 113.49$

In the statistical analysis performed by SAS Enterprise Guide 7.1 (SAS Institute Inc., Cary, NC, USA) the DON values from spray inoculation experiments were normalized with square root transformation. In the analysis of DON accumulation or *Fusarium*-infected kernels, the model included genotype as fixed effect and the experiments and replicates nested within experiments as random factors.

supported by the findings of Langevin et al. (2004) who described oats to be highly resistant against the spread of infection in panicle. Since our results did not point a mechanism that would differently restrain *Fusarium* infection in a spikelet of a moderately resistant oat compared to susceptible oat, it is likely that the panicle structure is an important restricting factor. Moreover, in our field studies the difference in FHB resistance between these two genotypes seems to fade away (Hautsalo et al. 2020), which also support this view. In field conditions, the type I resistance can be contributed by escape mechanisms, such as earliness, that are not observed in the greenhouse tests and weak agronomical traits can increase susceptibility of exotic genotypes.

The fresh weight reduction in the spikelets point-inoculated with *F. graminearum* in comparison with the water control was 0.012 ± 0.015 grams (mean $\pm$ S.D., $p < 0.001$) and according to similar statistical analysis as was performed for the *F. graminearum* biomass, it did not significantly differ between the oat genotypes nor the experiments (Fig. 2). *F. graminearum* infection had a similar effect on the spikelet weight in both inoculation events, despite the fact that the second experiment had less fungal biomass. This suggests that for the accumulation of *F. graminearum* biomass some destructive events within the infected plant tissue are required that release water from the tissue and thus reduce the fresh weight. This can actually be seen from the visible symptoms in the inoculated spikelets at 6 dpi (Fig. 3), although these were not quantified visually. *F. graminearum* is a hemibiotrophic fungus with a relatively short biotrophic phase of less than 48 h (Gottwald et al. 2012). The shift into the necrotrophic phase involves mycotoxin production and leads to oxidative reactions and cell death (Audenaert et al. 2014), which probably are the cause for the necrotic symptoms in the inoculated spikelet tissue. Similar observations were reported by Willforss et al. (2020). In the future, image analysis and high-throughput phenotyping approaches (Simko et al. 2017) could be applied in this kind of studies to measure the spreading of the infection.

Fig. 3 Deterioration of plant tissue (loss of chlorophyll) in *Fusarium graminearum*-inoculated spikelets detected at 6 dpi. Deteriorating area is marked with a circle

The log-corrected *F. graminearum*/plant DNA ratio significantly ($p < 0.001$) explained the weight reduction values in both the experiments ($R^2 = 0.51$ in the 1st experiment and $R^2 = 0.31$ in the 2nd experiment, Fig. 2). In spite of the significantly higher *F. graminearum* biomass in the 1st experiment, the spikelet weight reduction was similar in the two experiments. If differences in spikelet weight between genotypes would exist, this relationship between the spikelet weight reductions and the increase in *F. graminearum* biomass could provide a convenient and cost-effective method to quickly assess whether there is resistance against the spread of infection within the inoculated floral tissue. This is of interest for oats and also for other cereals, since symptoms and fungal biomass seem to correlate well (Kumar et al. 2015). Relative weight loss has been used in spray-inoculated resistance studies as a resistance parameter in wheat (Martin et al. 2017) and in oat (Martinelli et al. 2014), and it is shown to have a clear correlation with infection severity in both of these studies. However, weight reduction has not been studied at spikelet level in cereals before. Larger set of genotypes need to be studied to see the relevance of weight reduction method and more time points should be added to see if differences between genotypes are introduced later during the host-pathogen interaction, since the difference in *F. graminearum* biomass between the two separate point inoculation experiments (Fig. 2) suggests that the interaction continues after weight loss. Argamak and Belinda would be an interesting pair for this kind of study, since the proteogenomic background of their resistance has now been enlighten (Willforss et al. 2020). In addition, measuring DON accumulation in the point-inoculated spikelets and weight losses and/or *F. graminearum* biomass in the spray-inoculated panicles would increase our understanding of the nature of resistance and would thus be essential in the future studies.

Timing of inoculation to the right developmental stage is crucial in future inoculation studies, because after the anthesis the degrading anthers within the florets can act as a source of nutrients for the fungus (Tekle et al. 2012). On the other hand, if the inoculation is done too early, the plant tissue is less developed and softer, which can make the fungal penetration easier. Young tissue is often susceptible to infections with hemibiotrophic pathogens such as *Colletotrichum* (Peres et al. 2005). Because ‘VIR7766’ reached anthesis later than ‘BOR31’, the oat genotypes were point inoculated on different days with two weeks interval in the 1st experiment, which may have led to small environmental differences during the infection for the two genotypes. Therefore, the 2nd experiment was planted so that we were able to select and inoculate both genotypes at anthesis on the same day, which gave clearly less variable results for the *F. graminearum* biomass. Large deviations from the mean of the relative amounts of *F. graminearum* in plant and fresh weight reductions suggest

that an adequate number of replications is also important for the reliability in point inoculations.

The point inoculations could also be used for testing the aggressiveness of different *Fusarium* isolates and comparisons of oat responses to these; since this method ensures that the spores of the fungus reach the susceptible inner parts of the floret. The contrasting responses of some oat genotypes to incidence of infected kernels, mycotoxin accumulation and germination capacity in inoculated field studies (Tekle et al. 2018, Hautsalo et al. 2020) suggest that the quantitative resistance in oats may be a combination of the effects of several (minor) factors and their interactions that are yet unknown to us. Considering that the resistance response of an oat genotype is a sum of several mechanisms acting simultaneously, methods for studying each of the contributing mechanisms separately are needed.

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Compliance with ethical standards

Conflicts of interest Authors declare no conflict of interests.

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