Received: 2 September 2021 | Accepted: 8 December 2021 | Published online: 25 January 2022

DOI: 10.1002/csc2.20688

Crop Science

ORIGINAL RESEARCH ARTICLE

Crop Breeding & Genetics

Effects of varying levels of cleistogamy on natural smut infection in oats

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Assigned to Associate Editor Jochum Wiersma.

Funding information
Federal Ministry of Food and Agriculture, framework of the Federal Organic Farming Programme, Grant/Award Number: 28AIN02A20

Abstract

Smut of oats, caused by *Ustilago avenae*, is an important disease in organic seed production and resistance breeding via seed inoculation is an elaborate routine in organic oat breeding. The life cycle of smuts is known to depend on open flowers, for example, spores of *Ustilago* ssp. need to settle inside the flower to start a next life cycle. Increasing the level of cleistogamy as a way to avoid initial infections instead of selecting for genetic resistance to the pathogens has previously been proposed to speed up and/or improve the breeding for resistance to *Ustilago nuda* in barley. In the present study, this concept of avoidance of infection by cleistogamy was evaluated for oat, using three experiments with 25, 64 and 49 oat lines, tested in the first year with artificial inoculation at one or two sites for smut resistance, and in the second year with saved seeds for smut incidence (SI). Generalized linear models were fitted to analyze the effects of environment, susceptibility (SUSC), cleistogamy index (CI), and infection pressure during flowering represented by the portion of smutted panicles in the first year. The results confirmed that cleistogamy reduces the smut infection of the derived seeds for up to 68%, influenced by the susceptibility level and environmental factors. We conclude that cleistogamy can, in addition to genetic resistance, be used to manage smut in organic production systems. For the usage of cleistogamy instead of physiological resistance, the types of cleistogamy and the required level of cleistogamy to reduce smut infection should be studied in more detail.

Abbreviations: AICc, second-order Akaike information criterion; AR, anther retention; CI, cleistogamy index; GHExp, greenhouse experiment; NUExp, nursery experiment; OFL, open flowering; SI, smut incidenceSI1 smut incidence (%) of the first year, after artificial inoculation of the seeds; SI2, smut incidence (%) of the second year experiments, based on saved seeds without seed inoculation; SUSC, susceptibility level; TEMP, mean temperature.

1 | INTRODUCTION

Loose smut of oats is caused by the *Basidiomycete* fungus *Ustilago avenae* (Pers.) Rostr. (U. *avenae*). Infected plants can be easily detected after ear emergence because the panicle tissue is almost completely replaced by the powdery brown spore mass which makes the panicle look completely scorched. Until the development of fungicidal seed treatments during the 1960s and 1970s, loose smut was the most devastating oat disease worldwide. Removing smutted panicles immediately from the fields and breeding for smut resistance were important measures of disease control until the usage of fungicidal seed treatments facilitated the control of seed-borne diseases in conventional farming. With the advent of organic agriculture and with the ongoing decrease of approved fungicides in the European Union, smut resistance became a target of oat breeding again. Resistance breeding against smut is strongly influenced by fundamental studies from Zade (1924, 1928), Reed et al. (1925, 1947), Nicolaisen (1931, 1934), Sampson and Western (1938) and Nielsen (1977).

According to several studies (Diehl, 1925; Gage, 1927; Kolk, 1930; Nicolaisen, 1934; Sampson, 1929; Tapke, 1948; Thiede, 1963; Zade, 1924), the life cycle of *Ustilago avenae* on its host (see Figure 1) starts with the transfer of spores from smutted panicles to floral organs including the pistil, the anthers, and the inner side of palea or lemma of healthy oat panicles. The spores overwinter together with the seeds and infect the oat seedling shortly after germination.

There are partly contradicting reports in the literature whether either resting mycelium, gemmae, or dormant spores are the main source of inoculum for seedling infection. Even though Thiede (1963) found further evidence for dormant spores as the main inoculum source, which inoculum source is more prevalent seems to depend on the experimental conditions. However, as long as dormant spores, resting mycelium or gemmae on the pistil, on anther residues or in the inner hull, are present, the infection of the coleoptile of the germinating seed is possible. The infection of the coleoptile occurs before its penetration of the hull (Diehl, 1925). Spores on the outside of the hull do not infect the seedling according to Zade (1924). The coleoptile is growing past the hulls at the tip of the grain that is often a harbor of anther residues, which are a preferred medium for smut spores to germinate and to develop resting mycelium and gemmae. This may explain the lower incidence of smutted panicles if tips of grains are cut before seeding (Zade, 1924). Once a germ tube of a clamydospore has penetrated the cuticle, it grows through the epidermal and parenchyma cells of the coleoptiles. In the coleoptiles and first internodes, the hyphae grow mainly intracellularly and in the first leaf intercellularly (Mills, 1966). About 14–17 d after sowing and before the internodes elongate, the branched mycelium reaches the growing region, except for the resistant type found in the oat cultivar Black Mesdag (Kolk, 1930; Mills, 1966).

Core Ideas

- Loose smut of oats is an important disease in organic seed production.
- The effect of cleistogamy on flower infection with smut was evaluated for oat.
- Cleistogamy in oats reduces the smut infection of the deriving seeds.
- For the usage of cleistogamy instead of resistance, some knowledge gaps need to be closed.
- Cleistogamy is a worthwhile research target in oats.

The possible reasons for the frequent epiphytotic incidence of oat smut are discussed in numerous studies (Zade, 1924; Diehl, 1925; Gage, 1927; Sampson, 1929; Nicolaisen, 1934; Tapke, 1948; Thiede, 1963). Main causes are weather conditions during flowering, affecting the level of flower opening and the germination rate of spores enclosed within the glumes. In general, in cool wet weather, the spores form tubes and sporidia, whereas under warm and dry conditions, mycelium is directly formed, and spores remain dormant (Tapke, 1948). So far, it is unclear which situation is more favorable for disease emergence in the next generation.

The infection of chasmogamous flowers is one crucial step of the life cycle of *U. avenae* (Figure 1). Falck (1908) and later studies (Diehl, 1925; Gage, 1927; Sampson, 1929) question if cleistogamous flowering can prevent the infection. An early discussion of this hypothesis was made by Diehl (1925), supposing a lower infection level of the more closed flowering cultivar Dippes Überwinder. Similarly, Gage (1927) and Sampson (1929) noted that oat flower may fail to open at pollination due to cool weather, thus excluding the entrance of spores into the flower and reducing smut incidence in the succeeding crop. Extended experiments to utilize cleistogamy as an avoidance mechanism against *Ustilago nuda* in two-rowed barley were made by Pedersen (1960). The comparison between pseudoresistance, a term used by Pedersen (1960), measured via anther counts, and infection tests including the pathogen displayed clear advantages for the former. However, effective fungicidal seed treatments introduced in the subsequent decades reduced the investment in resistance breeding. More recently, Sperlingsson (2004) found different smut susceptibility rankings of oat cultivars after natural flower inoculation versus artificial inoculation of seeds and assumed different open flowering (OFL) levels behind these differences.

In the present study, three oat panels with known levels of susceptibility against smut and a range of cleistogamy were tested for flower infection while growing in a smut resistance nursery. The intention of this study was to quantify influential factors of smut infection of saved seeds from plants grown within smut resistance nurseries under high infection

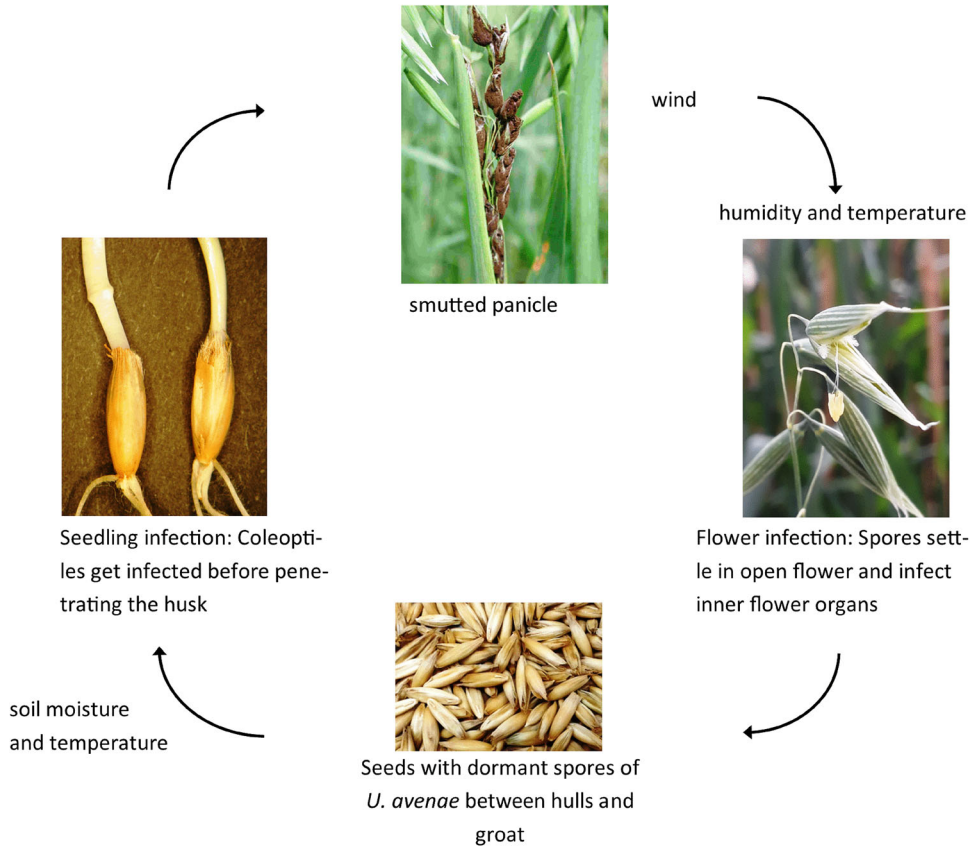

FIGURE 1 Illustrated life cycle of *Ustilago avenae* according to studies of Diehl (1925), Falk (1908), Kolk (1930), and Thiede (1963)

pressure. The focus was to elucidate whether closed flowering reduces smut infection and whether this avoidance mechanism can be used as an alternative to physiological resistance.

2 | MATERIAL AND METHODS

2.1 | Saved seeds origin

Seeds for the present study were taken from experiments of an oat project targeted on cleistogamy and resistance to smut. In this project, two panels (acronyms KLAR1 and KLAR2) each comprising 270 oat lines, were tested for smut resistance and flowering traits between 2017 and 2019 at sites in Quedlinburg (SITE1; 51°47′31.402″ N 11°8′29.213″ E, 140 m asl, loam), Groß Lüsewitz (SITE2; 54°04′15′′ N, 12°19′18′′ E; 37 m asl; sandy loam), and Bad Vilbel (SITE3; 50°11′39″ N, 8°45′10″ E, 119 m asl, silty loam). The seeds for the resistance tests were inoculated via vacuum-based infiltration using a smut spore suspension with 5 g spores per liter water and then dried afterwards. The inoculated seeds were seeded in a plot with two rows per replication, 90 cm long with a row distance of 20 cm and 40 seeds per row. We used an 18 × 15 rectangular lattice design for all field trials conducted with the two panels. To calculate the percentage of smut incidence in the first year (SI1), both smutted and healthy panicles were counted. To quantify anther retention (AR), eight panicles per plot were cut after flowering and stored at −20° C until counting the remaining anthers in the flower buds. The AR trait was calculated from the arithmetic mean of the number of anthers per flower retained in the glumes of four first-order flowers of each of eight panicles per plot. (Herrmann et al., 2020). The degree of open flowering was visually scored up to three times during the flowering period. We applied an OFL score of 1 (all flowers are closed) to 9 (flowers are wide open) based on the observed angle between the upper and lower glumes of the individual spikelets. For summarizing and statistical analysis, we used the maximum OFL value of the three scorings of a plot, since lower values could have been related to a too-early or too-late scoring daytime (see Discussion).

Due to the assumption that neither the AR nor the OFL traits alone characterizes the level of cleistogamy with sufficient precision, a cleistogamy index (CI) was calculated using both traits according to the following formula:

$$CI = 9 + 3AR - 0.5OFL \quad (1)$$

The higher weighting of the AR trait considers its higher precision and heritability. The uncertainty of OFL scoring was accommodated by the weighting factor 0.5. The addition of

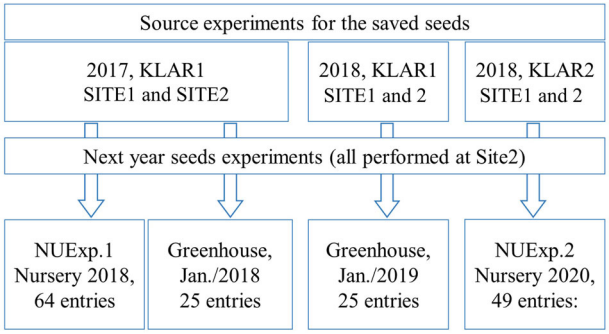

FIGURE 2 Overview for the experiments and panels used as saved seed sources for the second-year experiments

9 results in largely positive values for the CI, which was advantageous for data transformation steps and the visualization of the results.

2.2 | Experiments with saved seeds derived from plants subjected to flower infection

Saved seeds from healthy panicles of susceptible lines out of the first-year experiments were used for the so-called next generation experiments. Since susceptible lines were only useable for these experiments, we selected oats with a minimum level of susceptibility (SUSC) of 10% smutted panicles per plot. Susceptibility level was based on the mean smut incidence value of SITE1 and SITE2 2018 experiments, since these two environments enabled a maximum incidence level due to optimum infection conditions after seeding and germination. Beside the susceptibility, we selected oat lines with very different CI values to cover the complete range of CI. Overall, one greenhouse experiment (GHExp) and two nursery experiments (NUExp) were performed (Figure 2).

For the GHExps, 25 oat lines from panel KLAR1 were selected. In the nursery experiments NUExp1 and NUExp2, 64 oats out of KLAR1 and 49 oats out of KLAR2 were selected, respectively. For each selected oat line, we harvested healthy panicles that had flowered and matured beside smutted panicles within both replications of the experiments. Furthermore, each seed lot out of each plot from two replications per oat line was tested in two replications in the saved seed experiments. For the experiments NUExp1 and NUExp2, each sample was seeded in a plot consisting of three rows of 90-cm length with 50 seeds per row, resulting in a total number of 600 seeds for each oat line per site for the second-year tests. In the GHExp, the seeds were directly seeded in multipot trays (QuickPot 96T, Item No. 741238, Hermann Meyer), with 192 seeds per source sample and 1,536 seeds per genotype overall (2 samples per experiments × 2 experiments × 2 replications). The necessary sample size was estimated based on earlier experiments studying flower infection levels (Hermann, 2006) (Figure 3).

2.3 | Statistical analysis

The OFL-, AR- and CI-data were transformed via Box-Cox transformation (Box & Cox, 1964), and the data of the traits SI1 and smut incidence in the second year (SI2) were transformed by using the logit-function $L = \ln(p)/(1\text{-}p)$ to homogenize the error variances. In a next step, the data of the single experiments were analyzed using the BASIC and ANOVA commands in PLABSTAT version 3A (Utz, 2011), to gain basic statistical parameters and the heritabilities of the five traits.

For each separate experiment, as well as for the series (only the latter are shown for brevity), we fitted generalized linear mixed effect models with gamma distribution and log-link to analyze the severity of the smut incidence of SI2 using the glmmTMB package (Brooks et al., 2017) in R version 4.0.3. We first fitted a global model with CI, SI1, SUSC, EXP, and all two-way interactions (except for SI1 × SUSC) as fixed effects and SITE as random effect. We then applied the multimodel inference approach by Burnham and Anderson (2002) to select the most parsimonious models by fitting candidate models that were subsets of the global model using the dredge function of the MuMIn package (Barton, 2009). Smut incidence in the first year and SUSC were highly correlated within SITE and EXP; that is, a linear model with these variables resulted in a R^2 of 76.5. Hence, we fitted candidate models that only included one of the two variables. Candidate models were ranked by second-order Akaike information criterion (AICc). Akaike weights (w_i) and sum of Akaike weights (Σw_i) were used to estimate the relative importance of models and predictor variables (Burnham & Anderson, 2002). We interpreted the effects of all models within delta AICc <4 compared with the best fitting model. Models were interpreted using the effects package (Fox & Weisberg, 2019) and plotted with the ggplot2 package (Wickham, 2016).

3 | RESULTS

The majority of the assessed traits showed significant skewness and kurtosis, which was not fully solved in all cases by transformation (results not shown). The heritability of the traits ranged from 0.52 to 0.88 in the three experiments, suggesting relevant contributions of genes to trait expression, even if they are component traits such as CI, which was deduced from OFL and AR.

The saved seeds were derived from nurseries with quite different weather conditions at flowering and SI levels displayed in Table 1. There was a very dry spring and warm

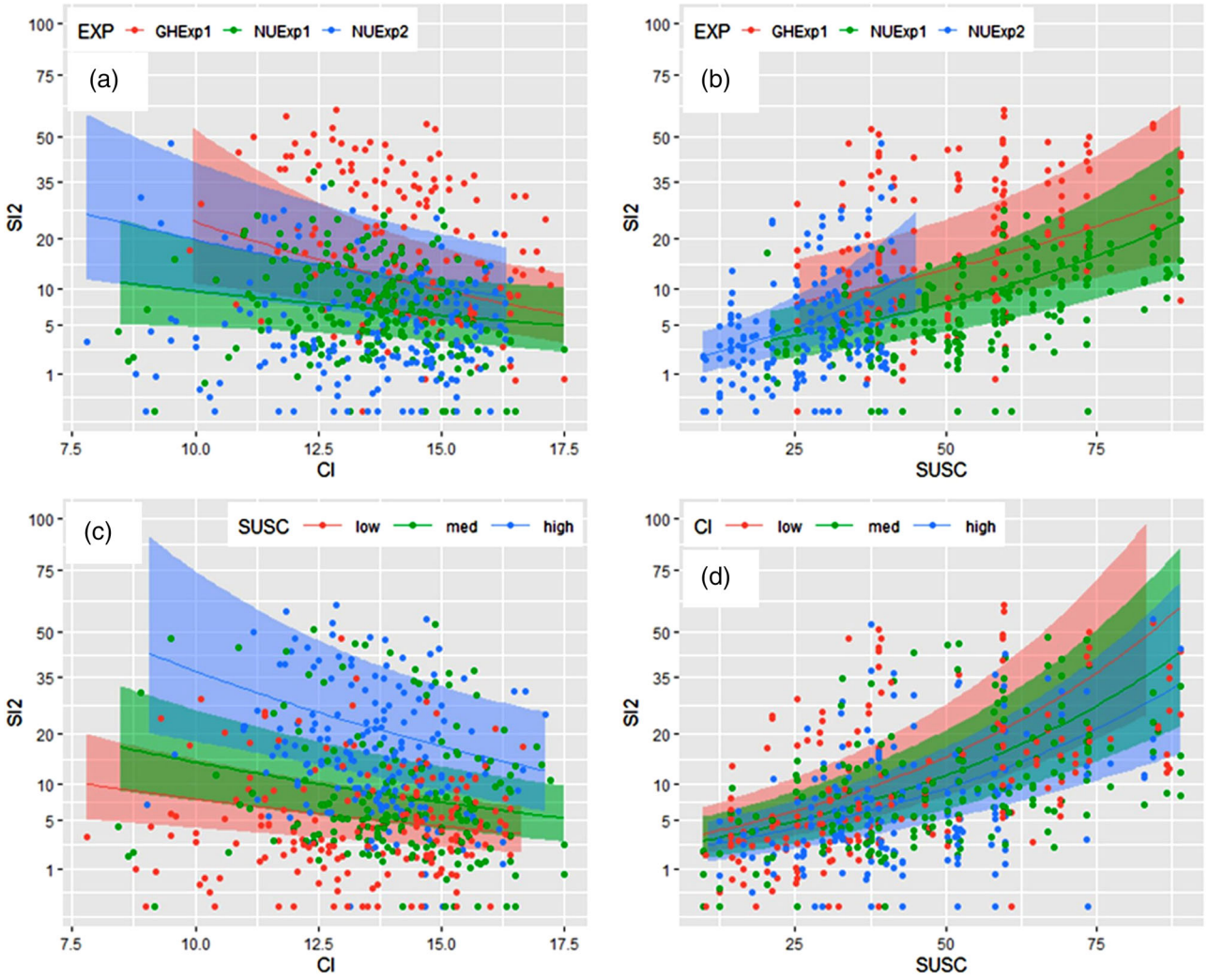

FIGURE 3 Effects of CI[†] (Figure 3a) and SUSC[‡] (Figure 3b) on SI2[$] for all three experiments. The lines depict best-fitting model predictions with shading indicating 95% confidence intervals. To visualize the interactions between the two continuous variables SUSC and CI, predictions were obtained for the 15-, 50-, and 85-percentile of CI (Figure 3c) and SUSC (Figure 3d), respectively, and categorized into low (red), medium (green), and high (blue) SUSC and CI. [†]CI = cleistogamy index. [‡]SUSC = susceptibility level (%) based on mean SI1 at SITE1 and SITE2 of 2018 experiments. [§] SI2 = smut incidence (%) in the second year

TABLE 1 Weather variables and mean values for smut incidence (%) in the first year (SI1) and cleistogamy index (CI), within environments Quedlinburg 2017 and 2018 (SITE1,17 and SITE1,18), Groß Lüsewitz 2017 and 2018 (SITE2,17 and SITE2,18), and Bad Vilbel 2018 (SITE3,18) of KLAR1 and KLAR2 panel smut resistance tests

Weather variables or trait	KLAR1				KLAR2	
	SITE1,17	SITE1,18	SITE2,17	SITE2,18	SITE2,18	SITE3,18
PREC_Germ	26.4	28.8	36.1	27.7	27.7	40.3
TEMP_Germ	7.7	13.5	6.2	11.2	11.2	14.8
Flowering start	15 June	07 June	20 June	10 June	10 June	08 June
PREC_Flower	59.0	4.6	138.9	38.6	38.6	27.9
TEMP_Flower	21.0	19.0	15.6	16.1	16.1	19.6
SI1	24.5	36.8	15.9	38.0	46.6	12.2
CI	13.1	12.9	13.5	15.6	13.9	13.2

Note. Weather variables are precipitation sum (mm; PREC_Germ) and mean temperature (˚C; TEMP_Germ) from 7 d before seeding until 14 d after seeding, and PREC_Flower (mm) and TEMP_Flower (˚C) are precipitation and temperature during flowering period of 14 d, respectively.

TABLE 2 Analysis of deviances for the most relevant factors within the fitted multiple regression models for the three single experiments

	GHExp				NUExp1				NUExp2			
Factor	**Chisq**	**df**	**Pr(> Chisq)**		**Chisq**	**df**	**Pr(> Chisq)**		**Chisq**	**Df**	**Pr(> Chisq)**	
CI	14.53	1	1.381E-04	***	5.30	1	.021	*	11.67	1	6.353E-04	***
SUSC	29.97	1	4.386E-08	***	26.79	1	2.26E-07	***	15.63	1	7.688E-05	***
SI1	5.79	1	1.613E-02	*	24.56	1	7.19E-07	***	0.03	1	8.685E-01	
SITE	45.22	3	8.302E-10	***	2.62	1	.1054		19.42	1	1.047E-05	***
SI1*SITE	16.71	3	8.128E-04	***								

Note.CI = cleistogamy index; GHExp, greenhouse experiment; NUExp, nursery experiment; SI1 = smut incidence (%) in the first year; SUSC = susceptibility level (%) based on mean SI1 at SITE1 and SITE2 of 2018 experiments.
*Significant at the .05 probability level. **Significant at the .01 probability level. ***Significant at the .001 probability level.

TABLE 3 AICc, delta AICc, and Akaike weight of the best fitting candidate models (dAIC < 4) and the null model to explain SI2

Model No.	**Model**	**AICc**	**delta AICc**	**Akaike weight**
Top1 model	SI2 ~ EXP + CI + SUSC + EXP*SUSC + (1 | SITE)	3370.1	0.00	0.60
Top2 model	SI2 ~ EXP + CI + SUSC + EXP*SUSC + CI*SUSC + (1 | SITE)	3371.8	1.70	0.26
Top3 model	SI2 ~ EXP + CI + SUSC + EXP*CI + EXP*SUSC + (1 | SITE)	3373.0	2.80	0.14
Null model	SI2 ~ 1 + (1 | SITE)	3504.1	134	0.00

Note.AICc, second-order Akaike information criteria; CI = cleistogamy index; dAICc, delta second-order Akaike information criteria; EXP, experiment; SI1 = smut incidence (%) in the second year; SUSC = susceptibility level (%). Models were fitted with gamma family and log-link.

summer in 2018 in SITE1 and SITE2, pushing SI1 level to 100% in some plots and up to nearly 40% overall compared with 20% in 2017. Additionally, the extraordinary drought in SITE2 2018 over the flowering period resulted in higher CI due to reduced anther extrusion and flower opening. Interestingly, CI remained low for SITE1 and SITE3, even with higher temperatures and lower precipitation during flowering 2018 compared with SITE2, which may be related to different soil water capacities at the different sites.

Thanks to very different environmental conditions over the three experiments, a robust picture of the influence of the tested factors on SI2 was deducible. In all three experiments, model factors CI, SITE, and SUSC displayed significant effects on the dependent variable SI2. For SI1, an inconsistent effect on SI2 was found for the single experiments, spanning from a significant effect in NUExp1 to nonsignificance in NUExp2 (Table 2).

Viewing the model analysis for the series, the multimodel inference revealed three best models within dAICc <4 (Table 3). All best models included the effects of CI, SUSC, and EXP (all with $\Sigma w_i = 1$) and the interactions between SUSC and EXP ($\Sigma w_i = 0.93$). The second and the third best model additionally included the interaction between CI and SUSC ($\Sigma w_i = 0.32$) or between CI and EXP ($\Sigma w_i = 0.23$). The variable SI1 was included first in the fourteenth best model with dAICc of 34.1 and a $\Sigma w_i = 0$, indicating a lower importance of SI1 compared with SUSC (Supplementary Table A1 and A2).

The variable SI2 decreased with increasing CI (Figure 3). Smut incidence in the second year increased with increasing SUSC, but this differed between experiments, with low increases of SI2 in NUExp1 compared with GHExp and steepest increases in NUExp2 (but note the lower range in SUSC values for NUExp2, Figure 3b).

The interactions in the second and third best models indicated a stronger positive effect of SUSC on SI2 when CI was low (Figure 3d) and a higher effect of CI on SI2 when SUSC was high (Figure 3c). This means that in more open flowering panels, susceptibility had a greater effect on SI2, and in more susceptible panels, the effect of cleistogamy was stronger.

In addition to the model selection above, the question of the possibilities for lowering the flower infection by cleistogamy was of major interest. To answer this question, the ten most chasmogamous and cleistogamous oat lines were compared in the two trials NUExp1 and NUExp2 with regard to SI2, taking into account influential traits (Table 4).

This comparison was based on groups of oat lines with different CIs, which were significantly higher for the cleistogamous group. The influential factors SUSC and SI1 were not significantly different for the groups. Susceptibility and SI1 levels were higher for NUExp1 compared with NUExp2. This higher SUSC and SI1 for the oats in NUExp1 corresponded to a higher SI2 in this experiment. The target trait SI2 was lower in the cleistogamous group in both experiments, with a reduction of 68% in NUExp1 and 36% in NUExp2. With respect to the nonsignificance of the difference for SI2 between the

TABLE 4 Comparison of mean values over 10 most chasmogamous and cleistogamous oat lines in the NUExp1 and NUExp2 for CI, SUSC, SI1, and SI2

Traits	Mean value of 10 most chasmogamous lines	Mean value of 10 most cleistogamous lines	P($T \leq t$) one sided *T*-test with unequal variances
NUExp1			
CI	11.6	15.4	4.82E-13
SUSC	58.5	49.6	0.46
SI1	31.3	26.7	0.48
SI2	11.3	3.6	0.27
NUExp2			
CI	10.4	15.4	2.50E-14
SUSC	24.0	27.0	0.03
SI1	14.8	14.2	0.48
SI2	3.1	2.0	0.42

Note.CI = cleistogamy index; NUExp, nursery experiment; SI1 = smut incidence (%) in the first year; SI2 = smut incidence (%) in the second year SUSC = susceptibility level (%).

cleistogamous and chasmogamous groups, it should be noted that there were wide ranges for SUSC in both groups, contributing to high variances for SI2 (Supplementary Table A3).

4 | DISCUSSION

The main purpose of this study was to determine whether closed flowering lowers smut infections and whether this pseudoresistance, as described by Pedersen (1960), can be used as an alternative to the physiological resistance. The first assumption – that a reducing effect of closed flowering on smut infection exists – was confirmed by the results of this study. The multiple regression enabled a dedicated estimation of the effects of environments, SUSC, SI1, and CI on smut incidence in the next generation. The results show that SUSC is the main influential factor on SI2, followed by the effect of CI. The factor SI1, the first-year percentage of smutted panicles after artificial seed inoculation, is related to susceptibility but is additionally dependent on the soil condition (i.e., temperature, wetness) during germination. In this study, SI1 represents the infection pressure during flowering, and it was assumed that a high infection pressure would lead to higher SI2. This was found only in NUExp1, and not for GHExp and NUExp2. It seems that the effect of the infection pressure is either less relevant or is masked by other influencing factors.

For the usage of cleistogamy as pseudoresistance in oat breeding, some prerequisites would have to be fulfilled: (a) sufficient genetic variation for cleistogamy, (b) no negative effects of cleistogamy on important breeding traits, (c) a sufficient smut-reducing effect of cleistogamy under different environments and (d) an effective scoring method for cleistogamy. There was a wide genetic variation for cleistogamy, which can be considered as a quantitative trait with moderate heritability. For using cleistogamy as pseudoresistance, it will be important to evaluate which level of cleistogamy is necessary to effectively reduce smut infection. A very precise answer to this question cannot be deduced because of the strong influence of SUSC, SI1, and environmental factors. We found reductions for SI2 in the groups of the 10 most cleistogamous oats compared with the 10 most chasmogamous oat group in a range of 68% and 36% in NUExp1 and NUExp2, respectively. Interestingly, there are a few oats with very low levels of SI2 even within the chasmogamous group, which are not explainable by low SUSC or SI1 (Supplementary Table A3). This indicates that there may exist unknown factors influencing SI2. In the trials of this study with optimal conditions for seedling infection, the cultivar average showed a halving of infestation in SI2 compared with the previous year after artificial inoculation. The SI2 of 64 cultivars in the field in 2018 averaged 30% relative to the SI1. In the trials of Sperlingsson (2004), the SI2 was about half of the previous year's infestation, and in Herrmann (2006), SI2 was even significantly lower with 4.4% of SI1. Based on the present results, a clear reduction of the SI2 compared with the SI1 infestation can be achieved. Whether this reduction continues with each generation and tends towards zero depends on SUSC, CI, and environmental conditions but cannot be assessed, as results are lacking. However, it seems worthwhile to investigate this question, which would at the same time allow a more precise definition of the resistance level necessary to prevent smut under field conditions.

When considering the physiology and morphological causes of cleistogamy, in preliminary experiments we observed two different types. Firstly, we found a particular glume morphology in two oats, with a stronger overlapping of the glumes and indented lateral edges leading to a clasping of the spikelets by the outer glumes. Secondly, we found

a positive correlation between lodiculae size after flowering and the level of cleistogamy, indicating an impaired lodiculae function in the cleistogamous oats. For the clasping glume type of cleistogamy negative effects on hull content and hullability are likely, making these cleistogamy types unusable for milling oats. No negative effects are known for the lodiculae-dependent type, but this still needs to be investigated.

Scoring of cleistogamy (e.g., OFL or anther extrusion) in oats is challenging, since there is a short daily time frame from about 4 to 7 p.m. The assessment of OFL is difficult because the difference between not yet flowered or cleistogamous flowering sometimes cannot be assessed with certainty. Therefore, counting anthers is the most affordable and precise indirect trait to assess cleistogamy levels, since OFL types push out the anthers that in turn fall off mainly depending on the wind force.

There are many smut-resistant genotypes among modern as well as older oat lines. Among the 540 oat lines tested for smut resistance in the KLAR project (Herrmann et al., 2020a), 32% showed resistance. Similar high portions of resistant lines were found in other studies like Uniform Oat Performance Nurseries in Champaign-Urbana, IL or SaintPaul, MN, United States (https://oat.triticeaetoolbox.org/search/trials). The resistances are mostly race-specific and expected to be less durable. By using cleistogamy as a pseudoresistance, the durability would be intrinsically present and there would be no need for artificial inoculations for resistance tests. On the other hand, environmental conditions affect the cleistogamy and may lower the intended avoidance of smut infection. Prior to a more extensive use of cleistogamy, questions remain to be answered regarding the types of cleistogamy and the level of cleistogamy required to reduce smut infection. In addition, research related to cleistogamy in oats seems worthwhile, as both infection with smut and with *Fusarium* (Herrmann et al., 2020b) can be lowered, and cleistogamy may be protective against heat during flowering and may have a yield-stabilizing effect, as was found in rice (Koike et al., 2015; Wu et al., 2019).

ACKNOWLEDGMENTS

Financial support: This work was supported by the Federal Ministry of Food and Agriculture within the framework of the Federal Organic Farming Programme (grant number 28AIN02A20). Our special thanks to Andrea Strebe and Carolin Viktoria Vollmer for their important work and contributions to elucidating the causes and effects of cleistogamy.

Open access funding enabled and organized by Projekt DEAL.

AUTHOR CONTRIBUTIONS

Sophie Brodführer: Data curation; Investigation; Methodology; Writing – review & editing. Ben Schmehe: Funding acquisition; Investigation; Resources; Supervision; Writing – review & editing. Doreen Gabriel: Formal analysis; Methodology; Validation; Visualization; Writing – review & editing. Dana Janowski: Data curation; Investigation; Writing – review & editing. Matthias Heinrich Herrmann: Conceptualization; Formal analysis; Project administration; Supervision; Writing – review & editing.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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How to cite this article: Brodführer, S., Schmehe, B., Gabriel, D., Janowski, D., & Herrmann, M. H. (2022). Effects of varying levels of cleistogamy on natural smut infection in oats. *Crop Science*, *62,* 704–712. https://doi.org/10.1002/csc2.20688