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## Field investigation of topsoil moisture and temperature as drivers for decomposition or germination of sclerotia (*Sclerotinia sclerotiorum*) under winter-killed cover crops

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### ABSTRACT

Cover cropping provides versatile benefits for sustainable agriculture, but many cover crops are potential host plants for pathogens such as *Sclerotinia sclerotiorum* (Lib.) de Bary. Therefore, 14 cover crops were investigated for their interaction with sclerotia, topsoil moisture and temperature in two consecutive field trials in East Austria. In July, after the cover crops were sown, sclerotia were inoculated at 3 cm soil depth in two mesh tubes per plot with 1×1 mm and 3×10 mm mesh size and remained until March. Cover crops did not affect decay of sclerotia, but sclerotia declined faster in 3×10 mm mesh compared to 1×1 mm (75.7 and 54.7%; respectively). Degree days reached the required 500 °C for apothecia development in September in both years, but only in year 1 was topsoil moisture sufficient for apothecia development. Nonmetric dimensional scaling revealed that, among others, topsoil temperature in March was significant for sclerotia germination in spring and was independent of plant biomass. There are indications that Poaceae such as sorghum × Sudan grass and Sudan grass can stimulate early germination under cover crops, causing vulnerability of sclerotia to degradation. This could reduce the pathogen pressure for the subsequent irrigated cash crops.

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nonmetric dimensional  
scaling; disease control;  
white mould


## Introduction

Cover crops are acknowledged for their ability to protect the soil from erosion and nutrient depletion and for their support of sustainable agriculture (Couëdel et al. 2018b; De Baets et al. 2011; Wittwer et al. 2017), but little is known about their effects on plant pathogens. An important pathogen in this context is *Sclerotinia sclerotiorum* (Lib.) de Bary, a soil-borne fungus with a wide host plant range such as Fabaceae, Asteraceae and Brassicaceae and thus many common cover crops (Boland and Hall 1994; Peltier et al. 2012; Prudy 1979). The life-cycle of *S. sclerotium* (white mould) starts when shallowly buried sclerotia take up water to germinate and induce carpogenic infection by developing apothecia (Abawi and Grogan 1979; Bolton et al. 2006). This process is mainly dependent on topsoil moisture, topsoil temperature and light, and takes 20–100 days or 160–1720°C degree days (Hao et al. 2003; Mila and

Yang 2008; Sun and Yang 2000; Wu and Subbarao 2008). Sclerotia are thought to produce the highest number of stipes at a topsoil temperature of 10°C, apothecia at 15°C within a topsoil moisture of – 0.01–0.3 MPa (Hao et al. 2003; Wu and Subbarao 2008). These requirements allow sclerotia to germinate under average climate conditions in September in East Austria (long-term mean air temperature 1998–2019: 15.6°C) and October (10.6°C) and can infect cover crops.

Sclerotia can remain viable for many years, and crop rotation with non-host plants for four to five years can prevent sclerotia germination (Adams and Ayers 1979; Kurle et al. 2001; Peltier et al. 2012). The viability of sclerotia depends on burial depth, soil moisture, soil temperature, soil chemistry and soil biology (Adams 1975; Cosic et al. 2012; Duncan et al. 2006; Huang and Kozub 1994; Kurle et al. 2001; Rousseau et al. 2006; Warmington and Clarkson 2016). Considering soil moisture, Cosic

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et al. (2012) reported that under flooded conditions, the majority of shallow (5 cm) buried sclerotia degraded within six months during the growing season. According to Adams (1975) and Twengström et al. (1998), sclerotia degradation is further accelerated by alternating drying and rewetting cycles. In contrast, soil temperature alone has little effect on viability of sclerotia. Indeed, Matheron and Porchas (2005) showed that 42–77% of sclerotia germinated after 28 days at 40°C and – 100 MPa soil moisture, but germination was completely inhibited after 7 days in wet soil (> –0.02 MPa). According to Harvey et al. (1995), the ability to produce stipes that can then form apothecia is considered to be independent of sclerotia size with 1.1 apothecia-sclerotium<sup>–1</sup> of size < 4 mm and > 4 mm in a field experiment. In contrast, Taylor et al. (2018) found a large dependency of sclerotia size of 1.1 (< 2 mm), 2.5 (4–6.7 mm) and 11.9 apothecia sclerotium<sup>–1</sup> (<6.7 mm) under a controlled 15°C. The different results of Harvey et al. (1995) and Taylor et al. (2018) show the variability of sclerotia and illustrate the need for further investigation at a field scale.

The research on sclerotia is also of interest for semi-arid regions like East Austria, with irrigated cash crops such as soybeans (*Glycine max* (L.) Merr.) and an increasing irrigation area, due to climate change adaptation (Schönhart et al. 2014). In this context, the impact of cover crops on the fate of sclerotia is still unknown. Cover crops affect soil moisture, soil temperature, soil chemistry and light incidence by shading the soil surface (Bodner et al. 2007; Couëdel et al. 2018a, 2018b; Euteneuer et al. 2020; Zibilske and Makus

2009). Results of Couëdel et al. (2018a), Monteiro et al. (2012) and Warmington and Clarkson (2016) indicated that mulch and volatiles of specific Fabaceae, Poaceae and Brassicaceae can reduce the number of sclerotia in laboratory experiments. In addition, under field conditions, Civardi et al. (2019) showed, that Congo grass (*Urochloa ruziziensis* Germ. & Evrard), a lignin-rich Poaceae, can reduce apothecia in subsequent soybean by stimulating early germination, resulting in soil decontamination. In general, cover crops can improve biological activity (A'Bear et al. 2014; Ludwig et al. 2018; Roarty et al. 2017), which Adams and Ayers (1979) also found to have a major impact on the survival of sclerotia.

For this study, cover crops from different plant families were selected based on their host and non-host capabilities. The aim of this research was to investigate the ability of cover crops (i) to produce plant biomass under semi-arid conditions, (ii) to impact topsoil moisture and temperature (0–7 cm) and (iii) to interact with sclerotia decomposition and germination at a field scale.

## Materials and methods

### Experimental site and environmental conditions

Field experiments were conducted from July 2015 to September 2017 at the experimental farm of the University of Natural Resources and Life Science, Vienna (Austria) in Gross-Enzersdorf (48°11'58.2"N, 16°33'46.9"E). The farm is located in the Pannonian basin in the East of Austria with an annual precipitation of 538 mm, an average temperature of 10.6 °C with most precipitation during the growing season and is classified as semi-arid (EU 2011; Yaqub et al. 2011). The soil is characterised as a calcareous Chernozem (WRB 2014) with pH<sub>CaCl2</sub> 7.6 and contains 23.3 g kg<sup>–1</sup> of organic carbon; the field capacity is 0.32 cm<sup>3</sup> cm<sup>–3</sup> and soil texture (air-dried) is defined by 213.3 sand, 570 silt and 216.7 g kg<sup>–1</sup> clay (Yu et al. 2016). Climate data were logged on a 15 min basis by a meteorological station (Adcon A733, OTT Hydromet GmbH, Kempten, Germany). Degree days were calculated as cumulative daily mean air temperatures from August to following March (Sun and Yang 2000), minus temperatures during winter were set at 0°C.

### Experimental design and cover crops

Two annual field trials that examined the effects of cover crops on sclerotia decomposition and germination were conducted in a randomised complete block design with six replicates. Cover crops were sown in pure stands in 3 × 10 m plot size after the harvest of

**Table 1.** Cover crop cultivars and their potential as host plant for *Sclerotinia sclerotiorum* (Lib.) de Bary according to Prudy (1979).

Cover crop treatments	Plant family	Potential host plant
Black oat ( <i>Avena strigosa</i> cv. 'Luxurial')	Poaceae	No
Buckwheat ( <i>Fagopyrum esculentum</i> cv. 'Lileja')	Polygonaceae	Yes
Common vetch ( <i>Vicia sativa</i> cv. 'Hanka')	Fabaceae	Yes
Corn cockle ( <i>Agrostemma githago</i> )	Caryophyllaceae	Yes
Grass pea ( <i>Lathyrus sativus</i> cv. 'Merkur')	Fabaceae	Yes
Mustard ( <i>Sinapis alba</i> cv. 'Bea')	Brassicaceae	Yes
Niger seed ( <i>Guizotia abyssinica</i> cv. 'Mungo')	Asteraceae	Yes
Oat ( <i>Avena sativa</i> cv. 'Raven')	Poaceae	No
Oilseed radish ( <i>Raphanus sativus</i> var. <i>oleiferus</i> cv. 'Radical')	Brassicaceae	Yes
Phacelia ( <i>Phacelia tanacetifolia</i> cv. 'Lisl')	Boraginaceae	Yes
Quinoa ( <i>Chenopodium quinoa</i> cv. 'Zeno')	Amaranthaceae	Yes
Rye grass ( <i>Lolium multiflorum</i> var. <i>westerwoldicum</i> cv. 'Aubade')	Poaceae	No
Sorghum × Sudan grass ( <i>Sorghum bicolor</i> × <i>S. Sudanense</i> cv. 'King 61')	Poaceae	No
Sudan grass ( <i>Sorghum Sudanese</i> cv. 'Piper')	Poaceae	No
Bare fallow (control; kept weed-free)	–	–

winter rapeseed (*Brassica napus* L.) on the 13th July 2015 (year 1) and spring oat (*Avena sativa* L.) on 20th July 2016 (year 2). Plant residues were incorporated with a cultivator to a depth of 7 cm and with a second pass 10 days later.

Cover crops were seeded at a 12 cm row spacing in drill seeding (Plot seeder S, Wintersteiger AG, Ried, Austria; Table 1). Bare fallow plots, kept free of any plant biomass by hand-weeding, served as a control. Cover crops remained on the field until Mid-April the following year and were winter-killed by January, except rye grass (*Lolium multiflorum* var. *westerwoldicum*) and partly corn cockle (*Agrostemma githago*). Plant biomass was taken in early November in both years by cutting 0.25 m<sup>2</sup> aboveground. Plant dry mass was determined after 24 h by heating at 105°C.

During the growing season, from August to November and during the following March, topsoil moisture and temperature at 0–7 cm were measured per plot (WET-Sensor, Delta-T Devices Ltd, Cambridge, UK; calibration according to the manual) on a weekly basis.

### Sclerotia

Mycelia of *S. sclerotiorum* were maintained on a potato dextrose agar (PDA) plate at 24°C and obtained from a strain of *S. sclerotiorum* isolated from a sunflower field in Gross-Enzersdorf in 2014. Mycelial plugs from the PDA were transferred to autoclaved wheat kernels (*Triticum aestivum* L. cv. 'Capo') in polypropylene boxes (15 cm × 10 cm × 5.5 cm, length × width × height) and sclerotia developed to full maturity at 24°C in darkness within six weeks (Euteneuer et al. 2019). After seeding of cover crops in year 1 and 2, respectively, two sets of firm sclerotia with a size of 4–8 mm were inserted into mesh tubes of 1 × 1 mm and 3 × 10 mm mesh size to restrict or allow earthworm access. The mesh tubes were inoculated at two randomly chosen locations per plot at 3 cm soil depth. Both sets of sclerotia were excavated by the end of March year 1 and 2, respectively. All excavated sclerotia were counted and categorised as 'remaining' when without stipes, as 'germinated' with stipes and additionally number of stipes sclerotium<sup>-1</sup>.

### Statistical analysis

Cover crop biomass (square root transformed) was analysed using a two-way linear mixed model (2-way LMM) with the fixed effect cover crop treatments (14 levels; mustard, oilseed radish, oat, Sudan grass, sorghum × Sudan grass, rye grass, black oat, grass pea, common vetch, corn cockle, phacelia, quinoa, buckwheat, Niger

seed) and years (2 levels; year 1, year 2) and replicates nested within years were set random.

To determine the effect of cover crops on topsoil moisture over months, a three-way linear mixed model (3-way LMM) was performed with fixed effects cover crop treatments, years and months (5 levels; August, September, October, November, March). Random effects were fitted for replicates, plots and months as repeated factor.

A 3-way LMM was performed for remaining or germinated sclerotia in March. Fixed effects were factors, cover crop treatments, years and mesh size (2 levels; 1 × 1 mm, 3 × 10 mm). Random effects were fitted per replicate and plots as both mesh sizes were inoculated in one plot (Piepho et al. 2004). For the germinated sclerotia, the number of remaining sclerotia was added to the model as a covariate.

Plant biomass and sclerotia were analysed with function 'lmer' ('lme4' package; Bates et al. 2015) in R (R Core Team 2021). Compound symmetry was used as a variance-covariance structure for repeated measurements and the residual maximum likelihood (REML) method was used for estimation. For the analyses of variance, the function 'Anova' was applied using Wald-type *F*-tests and the Satterthwaite's method for denominator degrees of freedom and type III hypotheses. Topsoil moisture was analysed with the package 'nlme' (Pinheiro et al. 2021) and function 'lme' and REML. Analyses of variance was conducted with the function 'anova.lme (type = marginal)' using Wald-type *F*-tests and type III hypotheses. Function 'emmeans' (package 'emmeans'; Lenth 2021) was applied in multiple mean comparisons (Sidak; *P* < 0.05) for factor combinations. All data provided are mean values and standard deviation (mean, ±SD). Residual distributions were inspected visually by frequency of residuals and homogeneity of the variance by box plots of residuals per variable and residuals against fitted values per model.

Ordination for rank orders suitable of topsoil moisture and temperature based on the proportion of remaining and germinated sclerotia was obtained by non-metric multidimensional scaling (NMDS) (Paliy and Shankar 2016). Non-metric MDS was performed with package 'vegan' (Oksanen et al. 2020) and function 'metaMDS' with Bray–Curtis distances and was solved with a two-dimensional ordination with a stress score of < 0.1 after an interaction of 20 tries (Clarke 1993; Kenkel and Orloci 1986). Non-metric MDS plotting was done with package 'ggplot2' (Wickham 2016) and 'score' function to extract the results of the vector fitting by function 'envfit' (package 'vegan') with scaling 'species' for sclerotia data and 'site' for soil parameters and plant biomass.

## Results

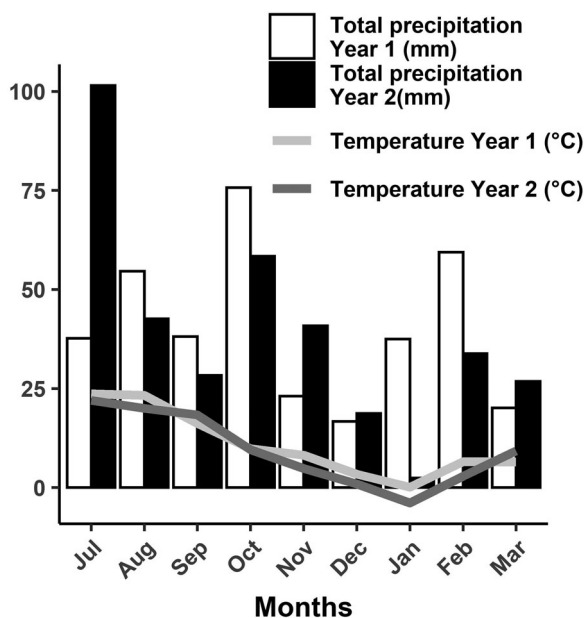
### Climatic data and cover crops

Total precipitation and mean air temperature from August to November were slightly higher in year 1 than year 2 (191.5, 170.1 mm; 14.3, 13.2°C; respectively; Figure 1). Additionally, the following months from January to March of year 1 had an increased precipitation and temperature of 117 mm and 4.3°C compared to year 2 with 63 mm and 2.7°C. Overall, year 1 resulted in higher degree days than year 2 and reached by the end of October 1510°C and by March 2371°C compared to year 2 with 1467 and 2079°C, respectively (Figure 2).

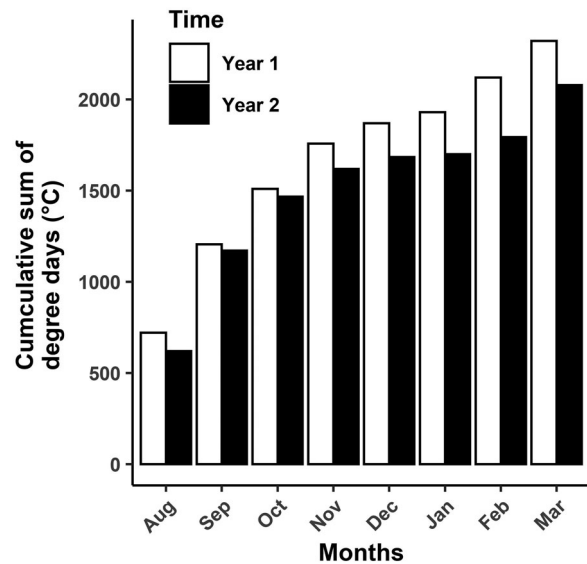
Cover crops gained higher biomass in year 1 than in year 2 ( $682 \pm 359$ ;  $72.2 \pm 76.3$  g m<sup>-2</sup>;  $F_1 = 57.1$ ;  $P < 0.001$ ) and differed between species ( $F_{13} = 19.4$ ;  $P < 0.001$ ) and showed interactions with year ( $F_{13} = 9.23$ ;  $P < 0.001$ ). In year 1, plant biomass increased with common vetch  $\geq$  remaining cover crops  $\geq$  corn cockle = mustard = black oat  $\geq$  Sudan grass > sorghum x Sudan grass (Figure 3) and in year 2 common vetch, buckwheat, corn cockle, rye grass had lower plant biomass than mustard, oilseed radish, black oat, oat and sorghum x Sudan grass (2-way LMM; Sidak;  $P < 0.05$ ).

### Topsoil moisture and temperature

Cover crop treatments, months and year showed an impact on topsoil moisture in the first seven centimetres and 3-way interactions (Table 2). Overall topsoil moisture

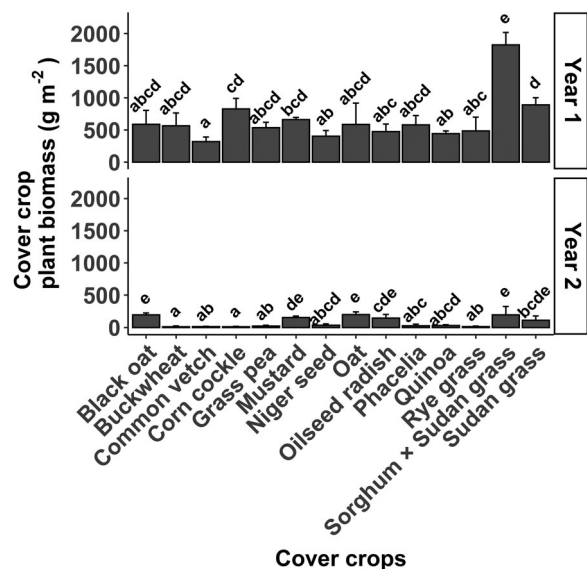


**Figure 1.** Climatic data with monthly mean air temperature (°C) and sum of precipitation (mm) from July 2015 (Year 1) to March 2017 (Year 2) at the study site in Gross-Enzersdorf (Austria).



**Figure 2.** Degree days for the duration of sclerotia (*Sclerotinia sclerotiorum*) inoculation from August to March in year 1 and year 2.

under bare fallow ( $6.46 \pm 2.28\%$ ) and oilseed radish ( $7.28 \pm 2.93\%$ ) were drier than under grass pea, rye grass, common vetch, Sudan grass and oat ( $8.19$ – $8.54\%$ ). Generally, topsoil moisture in year 1 was higher than year 2 and in detail August and October year 1 were moister than in year 2 and vice versa September, November and March of year 2 (Figure 4). In addition, interactions of cover crop treatments  $\times$  month  $\times$  year revealed buckwheat had drier topsoil than common vetch, corn cockle, oat, phacelia, rye grass and Sudan grass in



**Figure 3.** Aboveground plant biomass (g m<sup>-2</sup>) of cover crops in November in year 1 and year 2. Cover crops per year having no letter in common are significantly different by multiple mean comparison (2-way LMM, Sidak;  $P < 0.05$ ). Mean  $\pm$  SD,  $N = 6$ .



**Table 2.** Results of statistical analyses (3-way LMM) of topsoil moisture and temperature for five months from August to November and the following March under cover crop treatments (control [bare fallow], black oat, buckwheat, common vetch, corn cockle, grass pea, Niger seed, oat, oilseed radish, phacelia, quinoa, rye grass, sorghum × Sudan grass, Sudan grass) in two annual field trials (year 1; year 2).

Parameter	F-value	Df	P-value
Topsoil moisture (%)			
Cover crops (CC)	2.36	14	0.006
Months (M)	30.2	4	< 0.001
Year (Y)	12.1	1	0.006
CC × M	8.59	56	< 0.0001
CC × Y	2.23	14	0.009
M × Y	51.9	4	< 0.001
CC × M × Y	3.79	56	< 0.001
Topsoil temperature (°C)			
CC	1.85	14	0.038
M	546	4	< 0.001
Y	0.681	1	0.429
CC × M	0.815	56	0.829
CC × Y	1.29	14	0.219
M × Y	44.9	4	< 0.001
CC × M × Y	0.513	56	0.999

Note: Degrees of freedom (Df), *N* = 6.

August year 1 and bare fallow was driest in September – November year 1, August year 2 and following March in both years (Sidak;  $P < 0.05$ ; Figure 5; Supplementary table 1). Common vetch showed the highest topsoil moisture in September and October year 1, oat in November year 1 and Sudan grass in following March in both years (Sidak;  $P < 0.05$ ).

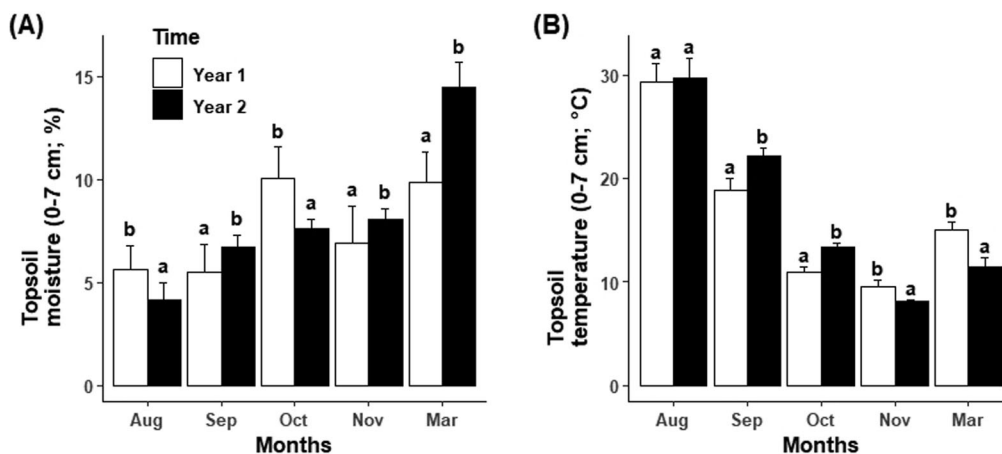
Three-way LMM analysis showed an impact of cover crops and month on topsoil temperature and interaction of month × year (Table 2). Overall topsoil temperature was higher under bare fallow ( $17.3 \pm 7.64^\circ\text{C}$ ) than sorghum × Sudan grass, Sudan grass, oat, phacelia, oilseed radish and buckwheat ( $16.5\text{--}16.7^\circ\text{C}$ ; Sidak;  $P < 0.05$ ). August, September and October topsoil

temperatures were warmer in year 2 than in year 1 and March year 1 soil was warmer than in 2017 (Figure 4).

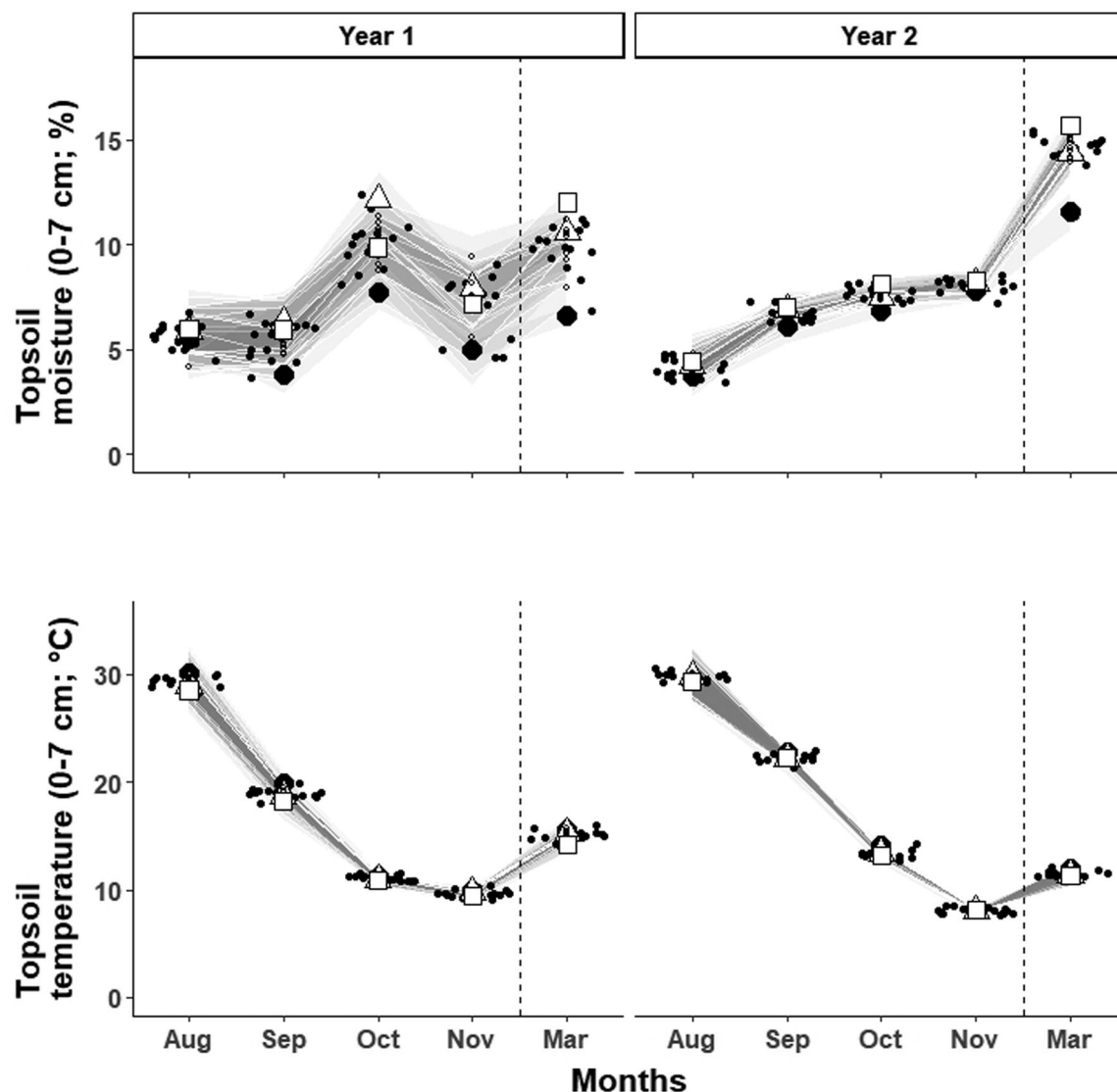
### Sclerotinia

Inoculated sclerotia were affected by mesh sizes and year in sclerotia decomposition and germination, but not by cover crop treatments (3-way LMM; Table 3). Overall, more sclerotia decomposed, when inoculated in  $3 \times 10$  mm mesh size than  $1 \times 1$  mm ( $0.24 \pm 0.22$ ;  $0.45 \pm 0.26$ ; respectively) and decomposition was higher in year 1 than in year 2. The number of germinated sclerotia differed between mesh sizes in year 1 and was highest in  $1 \times 1$  mm, but equal between both mesh sizes in year 2 (Sidak;  $P < 0.05$ ; Table 3; Figure 6). Additionally, the proportion of germinated sclerotia was independent of the covariate ‘remaining sclerotia’, as year 2 had higher abundance of remaining sclerotia than year 1, but lower numbers of germinated sclerotia (Table 3). However, in October year 1, single patches of infected plants were found in some stands of phacelia, mustard, corn cockle, grass pea and a few sclerotia were found on stems, flower heads and/or pods (Supplementary figure 1) and a few apothecia developed in the following March, but no apothecia or infected plants were seen in year 2 (Table 4). Number of stipes sclerotium<sup>-1</sup> only differed between years, but not in mesh size and was higher in year 1 than in year 2 (Sidak;  $P < 0.05$ ; Table 3; Figure 6).

In all, NMDS shows a clear separation of the two years along NMDS1 and assigns germinated sclerotia ( $1 \times 1$  mm:  $R^2 = 0.721$ ;  $3 \times 10$  mm:  $R^2 = 0.5$ ) to year 1 and remaining sclerotia to year 2 ( $1 \times 1$  mm:  $R^2 = 0.833$ ;



**Figure 4.** Topsoil moisture (0–7 cm; %) (A) and temperature (0–7 cm; °C) (B) from August to November and following March under cover crop treatments in two years (year 1; year 2). Month having no letter in common are significantly different by multiple mean comparison (3-way LMM; Sidak;  $P < 0.05$ ). Mean +SD, *N* = 6.



**Figure 5.** Topsoil moisture (%) and temperature (°C) of cover crop treatments of two years (year 1; year 2) for five months from August to November and March in the following year. Bare fallow (black dot), common vetch (white triangle) and Sudan grass (white square) are highlighted; details of the 3-way LMM and post hoc test (Sidak,  $P < 0.05$ ) are in supplementary table 1. Remaining cover crops (small black circles) are jittered by  $0.4 \times 0.4$  and dashed line indicates a sampling break during the winter. Mean  $\pm$ SD (grey shaded area),  $N = 6$ .

$3 \times 10$  mm:  $R^2 = 0.815$ ; Figure 7(a)). In contrast to higher numbers of remaining sclerotia in year 2, vectors (Figure 7(b)) show that soil parameter of year 1 affected sclerotia decomposition and germination by topsoil moisture in August, October year 1 ( $R^2 = 0.405$ ,  $R^2 = 0.472$ , respectively) and topsoil temperature in November ( $R^2 = 0.618$ ) and March year 1 ( $R^2 = 0.693$ ), whereas topsoil temperature in August year 1 and year 2 was indifferent to any finding. Plant biomass ( $R^2 = 0.404$ ) from November was assigned to germinated sclerotia in year 1 and seemingly did not interfere with germination in the following March.

## Discussion

To our knowledge, no research has been conducted on sclerotia decomposition or germination over the winter-time and with winter-killed cover crops in the current research area in Central Europe. Consequently, much of this research is compared with other climatic regions and strains of *S. sclerotiorum* with different pre-requisites and requirements. However, growing areas under irrigation in cash crops and narrow crop rotation, means that research like the current field trial is needed, as with rising temperatures the pathogen pressure can

**Table 3.** Statistical analyses (3-way LMM) of sclerotia decomposition (remaining), germination and stipes sclerotium<sup>-1</sup>.

Treatment	F-value	Df	P-value
<b>Remaining sclerotia</b>			
Cover crops (CC)	0.384	14	0.977
Mesh size (MS)	11.6	1	0.001
Year (Y)	10.2	1	0.002
CC × MS	1.01	14	0.458
CC × Y	0.466	14	0.947
MS × Y	1.00	1	0.320
CC × MS × Y	0.394	14	0.971
<b>Germinated sclerotia</b>			
Remaining sclerotia (RS)	0.33	1	0.565
CC	1.38	14	0.163
MS	0.558	1	0.456
Y	1.052	1	0.306
RS × CC	1.28	14	0.221
RS × MS	0.408	1	0.524
CC × MS	1.452	14	0.132
RS × Y	0.093	1	0.761
CC × Y	1.52	14	0.104
MS × Y	0.115	1	0.732
RS × CC × MS	1.63	14	0.073
RS × CC × Y	1.23	14	0.254
RS × MS × Y	0.002	1	0.969
CC × MS × Y	1.54	14	0.1
RS × CC × MS × Y	1.113	14	0.348
<b>Stipes sclerotium<sup>-1</sup></b>			
CC	0.244	14	0.998
MS	3.35	1	0.071
Y	9.72	1	0.002
CC × MS	0.449	14	0.952
CC × Y	0.373	14	0.980
MS × Y	0.786	1	0.387
CC × MS × Y	0.534	14	0.907

Note: Sclerotia of *Sclerotinia sclerotiorum* were inoculated in July for eight months under cover crop treatments (control [bare fallow], black oat, buckwheat, common vetch, corn cockle, grass pea, Niger seed, oat, oilseed radish, phacelia, quinoa, rye grass, sorghum × Sudan grass, Sudan grass) in two mesh tube sizes (1×1 mm, 3×10 mm) in two annual field trials (year 1: year 2). Statistical analyses of germinated sclerotia contains numbers of remaining sclerotia as continuous variable. Degrees of freedom (Df), F-value, P-value, N = 6.

increase (Garcia et al. 2005; Kurle et al. 2001; Peltier et al. 2012; Schönhart et al. 2014).

The cover crop biomasses were highly affected by plant species and year. In particular in year 1, this was in line with the ability of Poaceae to gain high plant biomasses (Creamer and Baldwin 2000; Duval et al. 2016). However, this could hardly be confirmed in year 2, when the cover crop biomass was clearly lower and nevertheless below the threshold of 3 t ha<sup>-1</sup> for sufficient weed suppression (Büchi et al. 2020; Gfeller et al. 2018; Wendling et al. 2019). In detail, common vetch gained lowest plant biomass (3.77 ± 0.99 t ha<sup>-1</sup>) in year 1 and developed slower than grass pea, as the latter is more tolerant to drier conditions and was above the threshold of 3 t ha<sup>-1</sup> (6.15 ± 1.5 t ha<sup>-1</sup>) (Biederbeck et al. 1993; Büchi et al. 2020). Further, Niger seed and buckwheat developed rapidly in both years, but were already terminated by frost at the time of

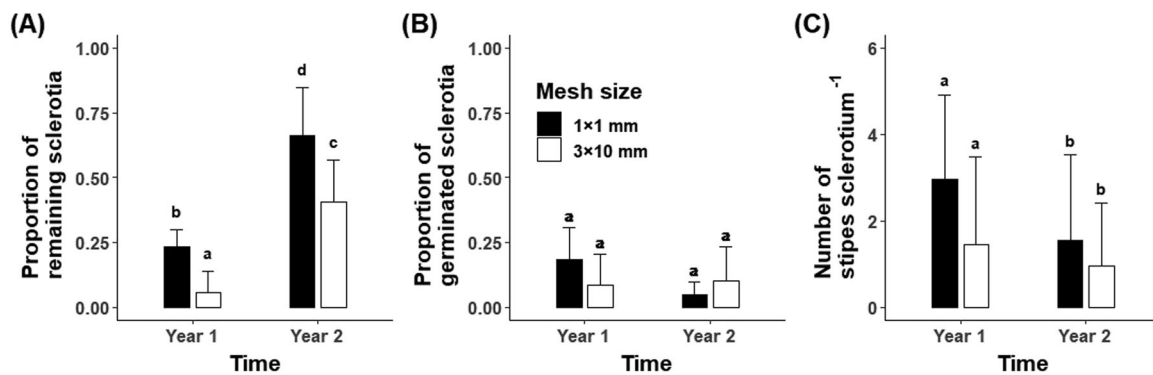
**Table 4.** Number of apothecia in March in year 1 in cover crop treatments. Mean ± SD, N = 6.

Cover crop treatments	Number of apothecia	±SD
Bare fallow	0.00	0.00
Black oat	2.00	3.46
Buckwheat	0.67	1.15
Common vetch	0.33	0.58
Corn cockle	1.00	1.73
Grass pea	1.67	2.89
Mustard	1.00	1.73
Niger seed	0.00	0.00
Oat	2.33	2.52
Oilseed radish	0.00	0.00
Phacelia	0.00	0.00
Quinoa	4.67	8.08
Rye grass	1.67	2.89
Sorghum × Sudan grass	5.67	7.37
Sudan grass	3.33	3.51

sampling in November and therefore lost plant biomass. In contrast, rye grass is an annual to biennial turf grass and known for usually high gains of plant biomass in the following growth season (Solomon et al. 2017). Hence, plant biomass production also affected evapotranspiration and topsoil conditions as seen with moisture and temperature throughout the year.

Over both years, cover crops affected topsoil moisture and were driest under bare fallow and oilseed radish compared to grass pea, common vetch, rye grass, oat and Sudan grass. Similar results were observed with Sudan grass, black oat, radish and bare fallow in the same study area by Euteneuer et al. (2020). The findings of Table 3 were related to dew formation and reduced evaporation from autumn to spring, due to shading of slowly decomposing Poaceae with a high C:N ratio and high biomass production (Blanco-Canqui et al. 2011; Xiao et al. 2009; Zibilske and Makus 2009). Despite cover crops affected topsoil moisture, their influence on the fate of sclerotia was negligible as shown in Table 3. The observed annual differences on decomposition of sclerotia was due to higher precipitation and degree days in year 1 compared to year 2 and not related to any specific cover crop treatment (Mila and Yang 2008). Also, Civardi et al. (2019) stated that the onset of germinated sclerotia was not affected by cover crop or spontaneous weeds in a field trial in Brazil. It is interesting to note the similar results in Congo grass in studies by Civardi et al. (2019) and in sorghum × Sudan grass as well as Sudan grass in the current trial. All three cover crops are relatively high in C:N and in the current trial sorghum × Sudan grass and Sudan grass had more apothecia by numbers in March year 1 than other cover crop treatments (except quinoa). That might be a function of their physiology and/or interactions with soil microorganisms, but it



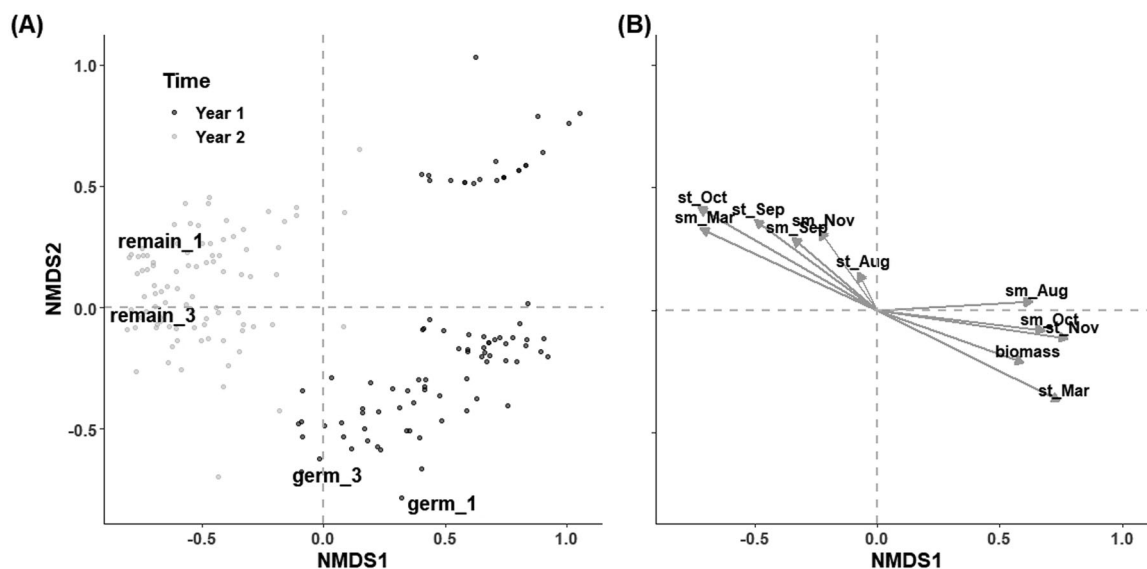


**Figure 6.** Proportion of remaining sclerotia of *Sclerotinia sclerotiorum* (A), germinated sclerotia (B) and stipes sclerotium<sup>-1</sup> (C) after eight months of inoculation under cover crop treatments (control [bare fallow], black oat, buckwheat, common vetch, corn cockle, grass pea, Niger seed, oat, oilseed radish, phacelia, quinoa, rye grass, sorghum × Sudan grass, Sudan grass) in topsoil (3 cm depth) in two mesh tubes (1 × 1 mm, 3 × 10 mm) of two years (year 1; year 2). Mesh size having no letter in common are significantly different in multiple mean comparison (3-way LMM; Sidak;  $P < 0.05$ ). Mean +SD,  $N = 6$ .

seems that Poaceae could be drivers for early germination of sclerotia.

More important than the effect of plants on the fate of sclerotia is soil moisture (Cosic et al. 2012; Mila and Yang 2008; Rousseau et al. 2006; Sun and Yang 2000) which may have been the limiting factor in year 2 (Abawi and Grogan 1979; Matheron and Porchas 2005). Increased topsoil moisture in the summer months of year 1 have facilitated the development of apothecia. These apothecia were indirectly detected by sclerotinia infections and mature sclerotia on stems and flower heads in single plants of phacelia, mustard, corn cockle, grass pea. Degree days in both years were within the given range

identified by Sun and Yang (2000) of 160–900 and 760–1720°C for high light (120–130 mol m<sup>-2</sup> s<sup>-1</sup>) or low light (80–90 mol m<sup>-2</sup> s<sup>-1</sup>). The light intensity under the canopy of the cover crops used in the current trial is unknown, but in both years, August reached > 500°C, September > 1000°C and October 1467–1510°C. This excludes temperature as a limiting factor and leaves lower soil moisture in year 2 responsible for the lack of any apothecia in autumn year 2. However, the generally low number of infected plants in year 1 might be related to findings of Mila and Yang (2008), that in a shorter time period more sclerotia germinated and developed apothecia with fluctuating temperature between



**Figure 7.** Nonmetric multidimensional scaling (NMDS) of (A) remaining sclerotia (remain) of *Sclerotinia sclerotiorum*, germinated sclerotia (germ). Sclerotia were inoculation in two mesh tubes (1 × 1 mm [\_1]; 3 × 10 mm [\_3]) under cover crop treatments in 3 cm depth of two years (year 1; year 2). Site parameters of NMDS (B) with aboveground cover crops biomass (biomass) and monthly mean topsoil moisture (sm) and temperature (st) from August to November and following March.

20 ± 4°C than between 20 ± 6 or 20 ± 8 °C in a constant water saturated soil. In the current trial, the range of night and day temperatures reached from 15 to 33°C at the beginning of September, 12–20°C in mid-September and 7–17°C by the end of September, which could have resulted in low numbers of apothecia and would explain why weekly field observations have failed to detect apothecia.

Overall, the poor plant establishment in year 2 was due to high temperatures and inadequate soil moisture by the end of July. The single heavy rain event by early July was not sufficient to facilitate cover crop germination; therefore, weed pressure increased and led to reduced cover crop biomass production. Cover crop treatments had no impact on sclerotia and higher plant biomass from November in year 1 than in year 2 did not interfere with the higher number of stipes in the following March year 1 as shown in Table 3. Overall, counted 0.96–2.96 stipes sclerotium<sup>-1</sup> in year 1 and in year 2 are in line with results from Harvey et al. (1995) with 1.1 apothecia sclerotium<sup>-1</sup> in a field trial. However, NMDS analyses revealed that topsoil moisture of August and October year 1 and soil temperature of November and March year 1 contribute to sclerotia germination in the following March. This finding accords with Workneh and Yang (2000), who identified temperature as essential for apothecia development when soil moisture is sufficiently available and close to field capacity. In the current trial, the soil at the critical time in March was not saturated, but considering the low winter temperatures from January to March (4.3°C in year 1 and 2.7°C in year 2) soil temperature was likely the more important factor for the development of apothecia in spring year 1 than soil moisture. Another indication for this conclusion is the reduced number of stipes sclerotium<sup>-1</sup> in March year 2, while the proportion of germinated sclerotia was similar in year 1 and in year 2. In addition, topsoil temperature in March year 1 was, despite the overall higher plant biomass in year 1 than in year 2, sufficient to produce apothecia also under high biomass crop sorghum × Sudan grass (1643 ± 381; 127 ± 113 g m<sup>-2</sup> in 2016; 2017; respectively). To investigate the germination during different months from autumn to spring would therefore be of interest. Additionally, NMDS showed that topsoil temperature (29.5 ± 1.91°C) in August alone had no influence on the germination of sclerotia. This can be related to the low topsoil moisture of 4.88 ± 1.23% in both years and is in line with Mathéron and Porchas (2005), where viability of sclerotia had not declined after 28 days with 40°C with – 100 MPa soil moisture. In general, cover crops proved their applicability for semi-arid areas related to topsoil moisture and their potential to diminish sclerotia pressure via

stimulation of early germination before subsequent cash crops. Nevertheless, most of the observed effects are related to annual weather conditions and cover crops might therefore be carefully selected in areas with higher rainfall during the late summer months. Therefore, cover crop mixtures with low plant density of mustard, phacelia, corn cockle and grass pea might be preferable for these areas.

Overall, numbers of sclerotia were reduced in 3×10 mm compared to smaller mesh size and Euteneuer et al. (2019) related this to activities of earthworms such as feeding on sclerotia, as seen with *Lumbricus terrestris* L. in a laboratory setting. In addition, likewise to mesofauna (Williams et al. 1998), earthworms could have contributed to the acceleration of sclerotia in 3 × 10 mm mesh tubes by the distribution of antagonistic fungi such as *Paraconiothyrium minitans*. However, these possible interactions of cover crops, earthworms and sclerotia ought to be investigated in further research and would add to the many benefits of cover crops.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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