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Disease suppressive soils vary in resilience to stress

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ABSTRACT

Soil-borne plant diseases are a major source of crop losses. Biologically active soils have the ability to suppress pathogenic infections of plants, but little is known how this essential soil function might be affected by abiotic stresses. Using a model system with pea and its fungal pathogen *Pythium ultimum* we studied how the suppressiveness of different soils from a wide geographic range responds to combined heat and drought stress. We found that different soils strongly differ in their ability to suppress diseases and that a stress event of combined heat (40 °C) and drought (−50% moisture) can strongly reduce this disease suppressiveness. Further, the response of suppressiveness to the stress depended on the provenance of the soil. Soils from a cool-climate site in Scotland were much more negatively affected than soils from warmer sites in Germany and Hungary. After being exposed to stress, one soil was able to regain suppressiveness after several weeks while the others were not, thereby collectively showing different degrees of resilience to the stress. Stress tolerance was negatively related to resilience. Our results suggest that microbial communities responsible for suppressiveness are adapted to prevailing climate, which has potentially severe consequences for the impact of climate change upon plant health.

1. Introduction

Soil-borne plant pathogens decrease the yield potential of all economically relevant crops across the world (Le et al., 2018; Marzano et al., 2015; van Toor et al., 2016), sometimes causing total yield loss (Okubara et al., 2014; Schroeder et al., 2006). In addition, soil-borne pathogens negatively impact cropping systems in indirect ways, e.g. by impeding the adoption of legume cropping, thereby reducing the potential of biological nitrogen fixation as an alternative to nitrogen fertilizers (Löbmann et al., 2016; Watson et al., 2017).

However, some soils are able to suppress diseases (Campos et al., 2016; Mazzola, 2002) by affecting the establishment, development and persistence of pathogens (Kwak and Weller, 2013; Mazzola, 2007). While abiotic soil characteristics including soil pH, moisture and clay content may play a role in suppressiveness (Jambhulkar et al., 2015), the main reason of suppressiveness is attributed to antagonistic mechanisms such as predation, parasitism, competition and antibiosis (Gómez Expósito et al., 2017). A well-studied example is the antagonism between *Pseudomonas* bacteria and the soil-borne fungal pathogen *Gaeumannomyces graminis* var. *tritici* causing the take-all disease in cereals (Weller et al., 2002). The suppressiveness of soils against plant diseases can be supported in various land management options, e.g. through organic amendments such as compost (Bonanomi et al., 2010; Pane et al., 2019).

While rising temperatures in the course of climate change are expected to increasingly disrupt crop production (Dawson et al., 2016; Wiebe et al., 2015) little is known about how soil suppressiveness may react to the projected changes (Chakraborty et al., 2012; Pautasso et al., 2012). So far, research has focussed on how plants or pathogens respond to (projected) climate change, e.g. the soil-borne oomycete *Phytophthora cinnamoni* (Burgess et al., 2017). A study modelling the response of *P. cinnamoni* to climate change assumed no reaction of suppressiveness to climate change (Thompson et al., 2014), but this assumption is currently not rooted in empirical evidence. In fact, van der Voort et al. (2016) demonstrated a change in the composition of the soil microbial community, especially bacteria, after heat treatment of

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the soil at 50 °C, and a concurrent loss of suppressiveness against the fungal pathogen *Rhizoctonia solani* (Mendes et al., 2011). Currently, however, it is unclear whether stress-induced loss of suppressiveness is also relevant under lower, i.e. more realistic soil temperatures, and in which way the tolerance of suppressiveness to stress varies among different soils.

In addition, soil microbial communities may also recover after the cessation of a stress event (Griffiths and Philippot, 2013). So far, the resilience of soils, i.e. their ability to regain functionality after stress has mainly been studied in terms of decomposition (Griffiths and Philippot, 2013), while other soil functions have been neglected in resilience studies. In view of the impact of soil-borne plant diseases on crop yields, and the key function of soils to reduce these diseases through various mechanisms of suppressiveness, it is essential to investigate the resilience of disease suppressiveness after stress.

This study therefore investigates the tolerance and resilience of the soil's ability to suppress plant diseases in response to abiotic stress in a model system based on a bioassay of a pea-*Pythium* pathosystem (Hagn et al., 2008) under controlled conditions in climate chambers. First, we compare soils from long-term experiments with different management and geographic origin across Europe for their ability to suppress the oomycete pathogen *Pythium ultimum* infecting pea (*Pisum sativum*) seedlings. In a second experiment, we analyse the tolerance of soil suppressiveness in response to combined heat and drought and the soils' ability to regain suppressiveness afterwards.

We hypothesise that (i) combined heat and drought stress negatively affects suppressiveness; (ii) tolerance of suppressiveness to this abiotic stress varies among different soils; and (iii) the ability to regain suppressiveness also varies among different soils. Specifically, after the stress event, we expected that the suppressiveness of the soil decreases initially, and recovers more quickly in some soils, in particular that soils with higher content in organic matter show stronger recovery.

2. Material and methods

2.1. Sample selection from long-term field trials

We used soils from active long-term field trials (LTFE) to ensure that soil properties are stable (Geisseler and Scow, 2014). The bioassays required large amounts of soil per trial, which restricted the selectable trials, because the long-term nature and value of the trials forbids exploitative soil sampling that would endanger the integrity of the trial for future studies. The selection of LTFEs was mainly based on plot size as a proxy for the possibility to take sufficient amounts of soil, but also on data availability, trial design, geographic range, variability in soil fertility, and identity of trial factors. Four LTFEs from three countries were chosen for the bioassays, with two treatments each. Two LTFEs were from Eastern Scotland (here abbreviated with 'Tulloch' and 'Woodlands'), one from North-Eastern Germany ('Thyrow'), and one from Eastern Hungary ('Westsik') (Table 1).

The Tulloch LTFE is the youngest trial with 25 years of continuous trialling at the sampling time for the present study and is conducted according to organic farming standards (Table 1). Management and soil properties are reported in **Table S1**. The other trials are run according to locally typical conventional practice, or modified as by the respective treatments. We selected two treatments from each of the trials to represent contrasting fertility levels within site, mainly according to previously obtained results on soil organic matter levels and crop yields.

In the pot experiments, samples from the two LTFEs that have field replicates (Thyrow and Tulloch) were pooled across replicates prior to using the soil in the replicated bioassays, because the available amount of soil was limited and by pooling the field repetitions equal inoculation of samples could be performed more precisely.

Although treatments were not identical between the different LTFEs, it was possible to group them according to their relative yield level (Table 2). Thus, within each site, level A represents the higher and level B the lower yield of a cereal test crop. However, the primary interest of the current study was not the comparison of different treatments on each site; instead, different treatments were selected to increase the variability of soil properties among the test soils.

2.2. Soil sampling, transport and sample preparation

Samples from the top soil (< 15 cm depth) were taken with hand trowels in spring 2016 (mid-March to beginning of April) from all four sites. The fresh soil was immediately put in plastic bags of approx. 20 l for transport in cooled containers from the sampling sites to the central testing facility at Kassel University, Germany. All soil samples were then stored at 5 to 7 °C until immediately before the start of the experiments. Before the tests, the soils were sieved (mesh size 10 mm).

2.3. Maintenance of pathogen and inoculation procedure

Soils were inoculated with different concentrations of a well-characterised, highly pathogenicisolate of *Pythium ultimum* isolated from sugar beet, as well as a *Pythium*-free control (Hagn et al., 2008). In parallel, all tests were also run with sand autoclaved at 121 °C for 20 min, as an additional substrate. For maintenance, the pathogen was grown on a 1.5% maize agar medium. The *Pythium* basic inoculum was propagated on a mixture of wheat-flour, sand and soil, which was diluted for the experiments to the necessary pathogen pressure to produce different disease levels for the host plants. Hence, inoculum levels are expressed per mil of the basic inoculum (‰ v/v) and further called '*Pythium* inoculum' (for further technical details see Electronic Supplementary Material).

2.4. Design of experiments and soil stressing

Peas (*cv*. Alvesta, non-treated conventionally produced seed from

Table 1
Characterisation of sites; all sampled soils are from long-term field experiments, further details see Table S1.

Site name	Woodlands	Tulloch	Thyrow	Westsik
Country	UK	UK	Germany	Hungary
Latitude	57°11′00″N	57°10′35″N	52° 16′ N	47°58′36″ N
Longitude	2°12′01″W	2°15′32″W	13° 12′ E	21°42′20″ E
Altitude (m asl)	125	125	40	103
Annual temperature (°C)[a]	7.9	7.9	8.9	10.0
Mean July temperature (°C)[a]	14.1	14.1	18.3	20.5
Annual precipitation (mm)[a]	816	816	495	618
Trial name	Old rotation	Organic rotation trial	Static nutrient depletion trial	Westsik rotation experiment
Start year	1922	1991	1937	1929
Soil type	Dystric Cambisol	Leptic Podzol	Albic Luvisol	Arenosol
Soil texture	Sandy loam	Sandy loam	Silty sand	Sand
Reference	(Walker et al., 2014)	(Watson et al., 2011)	(Ellmer and Baumecker, 2005)	(Lazányi, 2000)

[a] Multi-annual average, 1971–2000.

Table 2
Treatments selected for soil bioassays in experiments 2 and 4; sites are sorted by decreasing C_{org}-level, and within sites by descending relative yield level.

Criterion	Woodlands		Tulloch		Thyrow		Westsik	
Treatment	A	B	A	B	A	B	A	B
Original treatment name	3	5	T3	T4	a3	a8	X	I
Treatment explanation[e]	NPK	PK	Mixed	Stockless	NPK + FYM	PK	FYM	Control
Cereal yield (%)	100	92.8[a]	100	87.4[b]	100	17.7[c]	100	48.2[d]
pH (in H_2O)	6.0	6.9	6.0	6.1	6.8	7.0	6.0	5.4
C_{org} (%)	4.10	4.34	2.94	2.94	0.55	0.25	0.41	0.26

[a] Spring oats (Walker et al., 2010).
[b] Spring oats (Watson et al., 2011; Watson et al., 2015).
[c] Spring barley.
[d] Winter rye.
[e] Full treatment description see Table S1 in Supporting information.

KWS, Germany) were sown in 500 ml pots (5 seeds per pot, sowing depth 2 cm.). All four experiments were run in a randomized complete block design with five replicates. In experiment 1, eight test soils (2 treatments from each site, Table 2) were inoculated with 0, 2.5, and 7.5‰ of *Pythium* without prior stressing of the soil. For details on inoculation methods see Electronic Supplementary Material. In addition, in order to ensure robustness of the testing system, sterile sand was also included as a further substrate in this experiment. In experiment 2 we subjected all eight test soils from the four LTFEs to stress or non-stress conditions and selected two recovery times (1 and 43 days after the stress event). All soils were then inoculated with 0, 2.5, and 7.5‰ of *Pythium*. Again, sterile sand was included as an additional test substrate.

Subjecting the soils to the abiotic stress event was performed before pathogen inoculation and was done by using controlled heat (40 °C) vs. 15 °C in non-stressed soils, and drought (−50% of moisture content, w/w) vs. no loss of moisture in non-stressed soils. Stress conditions were maintained for a period of 4 days (96 h), with subsequent return to baseline temperature (15 °C) and moisture. For the period of the stress event, stressed and non-stressed soils were kept in open aluminium trays (dimensions 30 × 23 × 6 cm, 2 l soil per tray, 4 cm filling depth). Non-stressed soils were occasionally sprayed with water during the 4-day period to avoid drying out of the surface. Full re-wetting of the soils after stress was done carefully with a hand-held sprayer (from Gloria Haus- & Gartengeräte, Witten, Germany) in 50 l containers to return back to pre-stress water content. Over the four days, the non-stressed soil lost only small amounts of water (0% to 2.5% w/w), which were also compensated by rewetting. The choice of stress temperature followed other studies on the resilience of soils (Griffiths et al., 2001; Kuan et al., 2007; Wertz et al., 2007).

2.5. Testing and assessments

Pots were kept in three growth chambers with a daily regime of 16 h at 20 °C and 10.000 Lux, and 8 h at 16 °C in the dark; irrigation was performed as required. Per individual treatment combination, five replicates (pots) were randomized within the growth chambers. Plant growth was monitored daily. 21 days after sowing, the proportion of diseased peas was counted and the biomass of above ground parts of the plants was weighed. Disease severity was also scored and measured (as length of lesions) in selected treatments, following established protocols (Pflughöft, 2008). Note that the duration of the experiments from sowing onwards was always the same and did not vary with the different recovery time treatments. Mortality of pea plants was considered as the main parameter of interest. Mortality was assessed as the percentage of dead peas relative to the number of sown peas.

2.6. Calculations and statistical analysis

Mortality data was analyzed using a binomial error structure based on the number of peas, and in case of over-dispersion with quasi-binomial models. In some rare cases when mortality was 100% in all five replicates, i.e. when standard errors were 0, the analyses were supplemented with non-parametric Wilcoxon rank sum tests. The relative change y of plant dry matter in response to the inoculation was calculated as

$$y = (x_i - x_0)/x_0,$$

where x_i is the dry matter in the inoculated treatment and x_0 is the dry matter in the non-inoculated treatment.

Tolerance of suppressiveness against stress was defined as the absolute pea plant fresh matter difference between the stress treatment and the respective non-stress treatment. Resilience of suppressiveness was defined as the absolute pea plant fresh matter difference between the 43 days and 1 day after stress treatment. In this case, resilience is equivalent to the recovery of suppressiveness over a given time.

Analyses of variance were performed on fresh matter, dry matter and the relative change of dry matter. Homoscedasticity was examined with the Fligner-Killeen test, and normality of model residuals with the Shapiro-Wilk test. In multifactorial trials, model reduction followed AIC as model selection criterion (Burnham and Anderson, 2002); non-significant terms were removed from the model. Multiple comparison tests were performed with Tukey's Honest Significant Difference test. All statistical calculations were performed with the programme R, version 3.4.2 (R Development Team 2017).

3. Results

Evidence of the soils' suppressiveness was found in experiment 1 (Fig. 1). Peas survived to different degrees, depending on inoculum level. In comparison to the non-inoculated control, the loss of plant dry matter was significantly greater in soils than in sterile sand (data not shown). In addition, differences among soils were evident. Pea mortality was lowest and loss of dry matter smallest in the soils from Westsik. Within sites, suppressiveness was not linked to general parameters of soil fertility in this experiment (Table 2); in particular, SOM levels within sites had no significant effect on relative loss of dry matter in experiment 1.

Experiment 2 showed the impact of the combined heat and drought stress on the suppressiveness of soils. When inoculated with *Pythium*, stressed soils exhibited a lower survival of plants (Fig. 2), a higher disease score and a lower fresh matter (Fig. S3) than non-stressed soils, but this effect was strongly and significantly dependent on site (Fig. 3, $P < 0.001$, Table S2). In particular, the Scottish soils (sites Woodland and Tulloch) were much more negatively affected by stress application than the German and Hungarian soils. Fertility treatments had no consistent effect, as they did not affect the pea mortality in this experiment except for Westsik, where the heat stress increased pea mortality only in the high fertility soil.

With regard to resilience, the picture was more complex. Significant

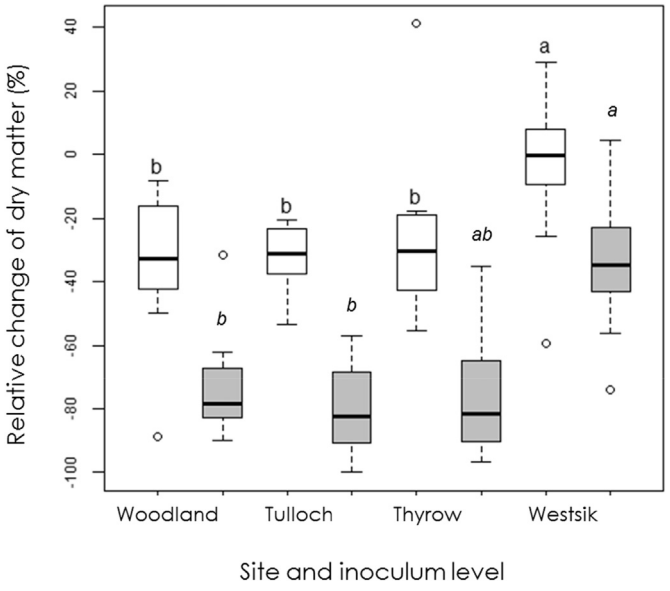

Fig. 1. Relative change of dry matter as percentage of non-infected treatment, depending on sampling site and on inoculum level (2.5‰, white boxes, and 7.5‰, grey boxes, experiment 2). A value of −100% equals complete loss of dry matter, so suppressiveness of the soils corresponds to deviation from −100%. Bars topped with different letters are significantly different within each inoculum level at $P < 0.05$ following Tukey's HSD test. Treatments within sites had no significant effect on relative change in dry matter in this experiment. Each treatment is shown with median (horizontal bold line), upper quartile Q_3 and lower quartile Q_1 (boxes), min(max(x)), $Q_3 + 1.5(Q_3–Q_1)$ (upper whisker), max(min(x)), $Q_1–1.5(Q_3–Q_1)$, (lower whisker), as well as outliers (circles).

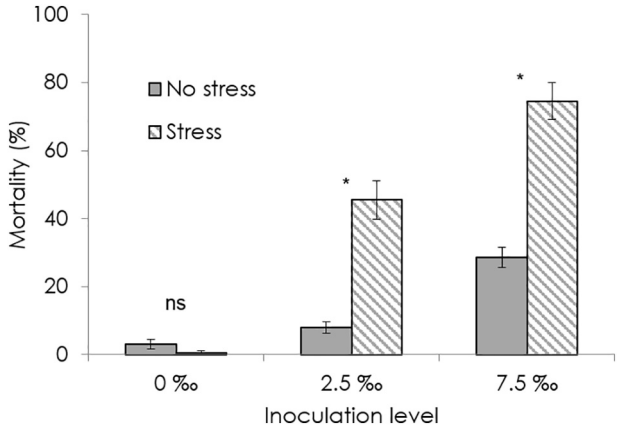

Fig. 2. Mortality of pea seedlings (% of sown), means and standard errors across eight test soils from the four sites, for three different *Pythium* inoculum levels in stressed (hashed bars) vs. non-stressed soils (solid bars) (experiment 4); sowing was done one day after stress or control event. Significance level of difference between stress treatments at each inoculum level, according to general linear model with quasibinomial error distribution: ns: not significant; *: $P < 0.05$; for full statistical analysis see Supporting Information. Mortality of peas in sterile (autoclaved) sand was 0%, 92% and 100% at 0‰, 2.5‰ and 7.5‰ inoculation, respectively (n = 5).

resilience of the ability to suppress diseases was only found in one out of eight soils (Tulloch B, Fig. 4a, difference between "day 1 soil" and "day 43 soil" significant, $P < 0.01$). In six other soils, there was no difference in suppressiveness between soils that had been stressed 43 days before and soils tested immediately after the stress event. In the Westsik B soil, the suppressiveness was significantly weaker 43 days after the stress event than 1 day after it (Fig. 4b, $P < 0.05$).

Further, there was a significantly negative correlation between resilience from stress (measured as plant fresh matter difference between 43 days and 1 day after the stress event) and tolerance to stress (measured as plant fresh matter difference between the stressed and the non-stressed treatment) (Fig. 5). There was no significant correlation between resilience after stress and SOM or microbial biomass.

4. Discussion

Our experiments provide evidence of suppressiveness in different soils against the model pathogen *Pythium ultimum* infecting peas (Figs. 1, S1, S2). Soil-borne diseases such as *Pythium ultimum* are a strong yield limiting factor in grain legumes such as peas (Finckh et al., 2015; Saeed et al., 2017; Seethapathy et al., 2017), thereby negatively affecting protein supply in food and feed, but also nitrogen supply in crop rotations (Reckling et al., 2016). Because soil borne diseases increase the necessary number of break years between successive legume crops (Döring, 2015), suppressiveness of soils has important indirect impacts in that it helps to maintain higher concentrations of legumes in crop rotations. Apart from legumes, however, suppressiveness of soils is also important in multiple other crops (Gómez Expósito et al., 2017). Confirming earlier research on suppressiveness of soils from long-term experiments (Tamm et al., 2010), we found that suppressiveness against *Pythium ultimum* was affected by the identity of the test soil (Fig. 1).

Further, we demonstrate that the disease suppressiveness of soils is negatively affected by combined heat and drought stress (Figs. 2–4), bearing particular relevance under conditions of a warming climate with an increasing prevalence of droughts and more extreme weather events. Our results are in line with a similar study which found reduced suppressiveness against the pathogen *Rhizoctonia solani* infecting sugar beet seedlings following shorter (1 h) and much stronger (50 °C and 80 °C) heat stress events (Mendes et al., 2011; van der Voort et al., 2016). As the results presented here demonstrate, suppressiveness can already be affected by lower temperatures, i.e. at 40 °C which lies within a more realistic bracket for soil surface temperatures (Ramier et al., 2009) than previously tested.

In our study it is not possible to disentangle heat effects from drought effects, but these two stress factors often co-vary anyway, because high temperatures increase evaporation and are associated with low precipitation. Previous research has shown that climate change affects plant diseases through multiple mechanisms (Pautasso et al., 2012), including accelerated evolution of pathogens, shorter periods of incubation, earlier incidence of first infections within the season, expansion of the geographic range of pathogen occurrence, and higher susceptibility of plants to diseases under abiotic stresses. Our results highlight a further mechanism how plant diseases can be affected by climate changes. As we show, a heat and drought pulse can lead to reduced ability of the soil to suppress diseases, which increases the severity of climate change impacts on plant health, and adds further complexity to the pathosystem.

In our study, different soils were affected differently by the stress (Figs. 1, 3, 4), which may be explained by variability in the composition of soil microbial communities (van der Voort et al., 2016). The Scottish soils were more negatively affected than the German and Hungarian soils. A plausible explanation for this observation is a differential adaptation of the microbial community to climatic situation (Table 1). High summer temperatures experienced by soil microbial communities at the Hungarian site may have pre-adapted them to the experimental heat (and drought) conditions. This means that soils from higher latitudes, where temperature increases are predicted to be stronger in the future will be particularly vulnerable to decreased suppressiveness against plant diseases. In the long run, soils may also adapt to changed climatic conditions.

Our experiments provide evidence of resilience of the suppressiveness function in one of the tested soils, the Tulloch B soil (Fig. 4). Previous research on resilience in soils has concentrated on only a few functions, with the main focus being on decomposition (Griffiths and

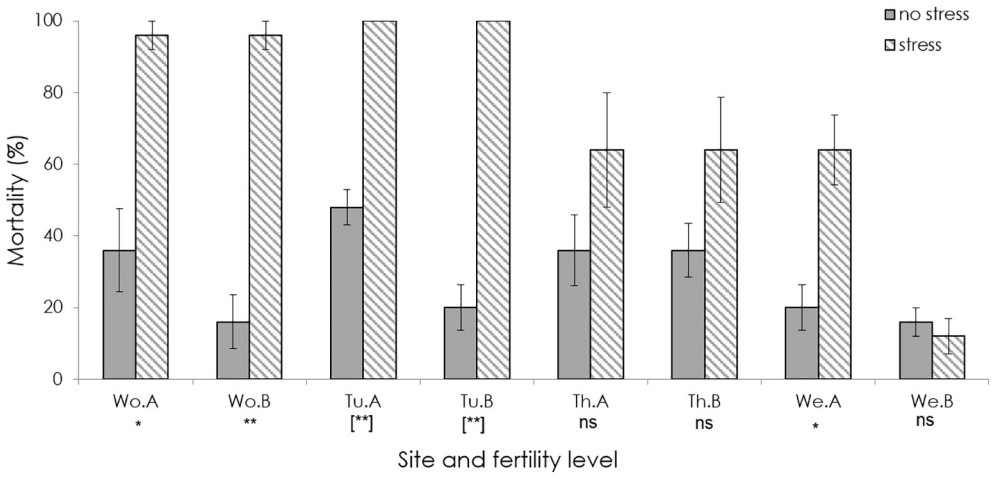

Fig. 3. Mortality of pea plants (means and standard errors, n = 5) in eight different soils which were inoculated with 7.5‰ *Pythium* (experiment 4). Soils were inoculated one day after keeping soils at 15 °C (solid bars) or after combined heat (40 °C) and drought stress was applied to the soils (hashed bars); Wo: Woodlands, Tu: Tulloch, Th: Thyrow, We: Westsik; A: High fertility; B: low fertility; significance levels for test between stressed and non-stressed soils as follows: *: P < 0.05; **: P < 0.01; ns: not significant according to general linear model with quasibinomial error distribution. Pea mortality in non-inoculated treatments was 3.0 ± 1.3% and 0.5 ± 0.5% in non-stressed soils and stressed soils, respectively.

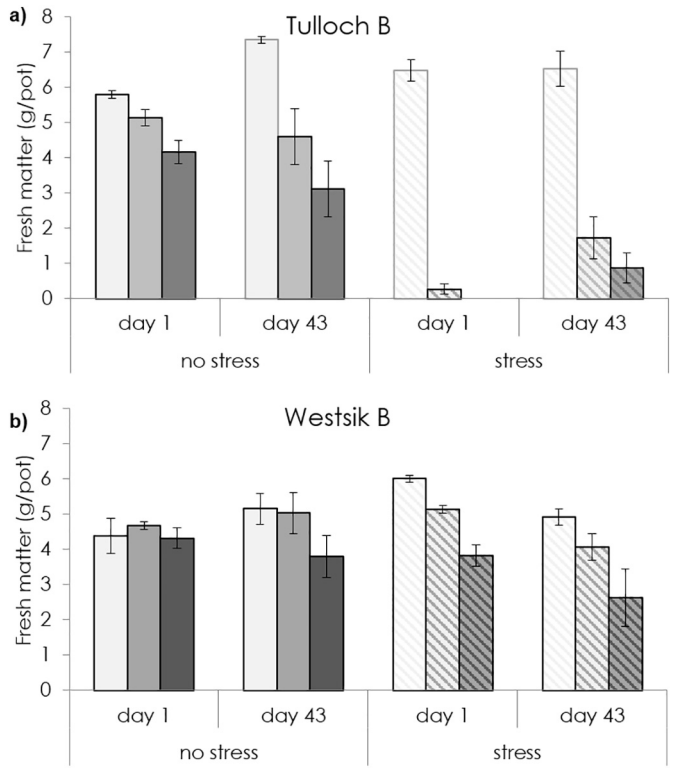

Fig. 4. Fresh matter of pea plants (means and standard errors, n = 5) on the Tulloch B (a) test soil and Westsik B (b) soil, depending on stress level and the number of days elapsed since the stress event (experiment 4); *Pythium* levels: without inoculation (light bars), 2.5‰ (intermediate bars) and 7.5‰ (dark bars). Note that the experimental design allows mortality to increase or decrease over time.

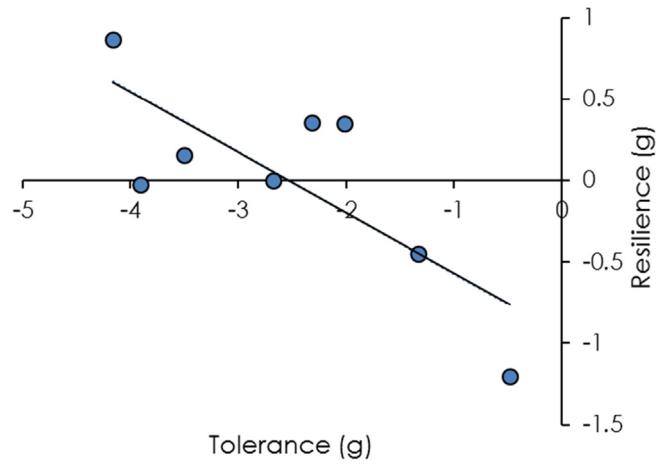

Fig. 5. Relationship between tolerance to stress and resilience from stress (experiment 4) with tolerance being defined as absolute pea plant fresh matter difference between stressed treatment and non-stressed treatment and resilience defined as absolute pea plant fresh matter difference between 43 days and 1 day after stress treatment; each point represents 5 replicates; adjusted $R^2 = 0.529$, $P < 0.05$, df = 6.

Philippot, 2013). To our knowledge, resilience of suppressiveness has so far not been investigated. Yet how quickly suppressiveness is regained in soils is highly relevant for crop production because of the relatively short time period in which plants are infected by soil-borne pathogens. Resilient soils may regain suppressiveness after a stress event before the susceptible period begins, thereby reducing the risk of disease infection, whereas less resilient soils could recover eventually from the stress, but recovery may be too late for plants to benefit from regained suppressiveness.

A conceptual model for the reassembly of the soil microbial community after heat stress was presented recently by van der Voort et al. (2016). According to this idea, microbial reassembly depends on two properties of the community tolerance against the stress and growth rate of individual species. Functionally, low stress tolerance can be compensated for by high growth rate. Insofar as a pre-requisite of high resilience is high growth rate for quick recovery, our results help to expand these ideas. The Westsik soil showed greatest stress tolerance (Fig. 3) but low resilience (Fig. 4), indicative of low growth rate after stress. The opposite was the case for the Tulloch soil, combining low tolerance to stress with a significant ability to recover from it. In fact, across all tested soils, tolerance was negatively correlated with resilience (Fig. 5), indicating a trade-off between tolerance against combined heat and drought stress and the ability to recover from such stress.

Because only one in eight tested soils showed significant resilience of suppressiveness, further research is needed to determine how widespread this phenomenon is in agricultural (and other) soils and on which factors it may depend. While the methodology developed for this study is able to generate robust results on suppressiveness, using it for testing resilience is also quite demanding in terms of experimental effort.

Both suppressiveness and the response of this function to stress were not positively affected by soil organic matter (SOM) content or other parameters typically associated with high soil fertility (Fig. 3). This was true within sites and among sites, i.e. the higher soil fertility treatments

within individual sites (e.g. with addition of farm yard manure) were not associated with higher suppressiveness or stress tolerance. For example, pea survival was greatest in the Westsik soils (Fig. 1), which showed lowest levels of soil organic carbon among the test sites (Table 2). Similarly, in a survey of 26 soils across Scotland, organic carbon content was not correlated to resilience after heat (Kuan et al., 2007). Microbial biomass (Table S1) was also not consistently correlated with suppressiveness (data not shown). These observations are unexpected, since addition of organic matter such as compost to soil is known to increase disease suppression, though different composts can affect diseases differently (Termorshuizen et al., 2006). The fact that in our study, soil suppressiveness and response of this function to abiotic stress was not associated with high SOM levels means that there may be a trade-off between different functions of biological parameters of soil fertility. In particular, previous research on resilience and response to (abiotic) stresses has focused on decomposition; our study suggests that this function may not necessarily be aligned with suppressiveness.

Recently Griffiths and Philippot (2013) suggested that resistance and resilience of the soil microbial community are governed by soil physico-chemical structure through its effect on microbial community composition and physiology. However, the effect of soil texture and structure on suppressiveness, resistance and resilience is not considered in most studies. Gregory et al. (2009) argue that soil biological and physical resilience is closely linked, as biological processes in soil depend on the physical pore structure that defines microbial habitats. In their study, grassland soils with high organic matter were more resistant and resilient to heat, copper and compaction than arable soils. An arable soil with 65% clay was found to be highly resilient also, pointing towards soil texture as another parameter affecting soil resilience. Kuan et al. (2007) found that soil resilience to heat stress could be distinguished by soil class, which is related to soil texture. Heijnen and Van Veen (1991) showed that addition of clay minerals increased survival of rhizobia inoculated into a sandy loam and attributed this effect to the creation of protective microhabitats, inaccessible to protozoa predating on rhizobia. Plant growth promoting rhizobacteria (PGPR) associated with suppressiveness, like e.g. *Pythium oligandrum*, which has been identified as one antagonist of *Pythium ultimum* (Martin and Hancock, 1986), could be better protected from heat in small pores. In turn, the soil fauna and microbial community may contribute to stabilize soil structure, e.g. via earthworm burrowing or fungal hyphae. How exactly soil structure is linked to microbial community composition, physiology and function, certainly needs further research. Thus, to shed light on the mechanisms underlying the detected differences in tolerance and resilience to abiotic stress, future studies should include soil structure and its interactions with soil microbes.

It needs to be noted that our experiments were conducted under relatively artificial conditions, which was partly due to the need to preserve the integrity of the long-term trials, and partly due to the desire to run the experiments under controlled conditions so that observed effects can be attributed to a known pathogen and the stress and recovery treatments. Further research is necessary to establish to which degree the observations are also valid in the field, with more variable environmental conditions, and more complex interactions with the soil biota. This is particularly important since microbial communities, and their ability to respond to, and recover from, stress will depend on the interaction with deeper, unstressed layers of the soil. Further, different plant pathogens may respond to realistic stress events in different ways. *Pythium*, which is known to affect seedlings especially in cool and damp conditions, may not experience strong heat or drought stress, but this pathogen species can probably stand as a representative for the consortia of fungal pathogens that affect (young) pea plants. Finally, a larger number of soils, analyzed more comprehensively for differences in microbiological parameters, will help to come closer to identifying the mechanisms that underlie the differences in dynamic changes of suppressiveness of soils in response to abiotic stresses.

Concluding, this study demonstrates that the ability of the soil to suppress diseases is affected by stress events, such as combined heat and drought stress which lead to short-term negative effects on plants by reducing disease suppressiveness of soils. This response strongly varies among different soils, with soils from sites with a high prevalence of climatic stress being affected more strongly but tending to show greater degree of resilience. While some soils are pre-adapted to stress, others may compensate their lack of adaptation by higher growth rates and regaining their suppressiveness faster after being stressed. The underlying mechanisms need further research.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

CB, CW, DR, IV, JK and TFD designed the experiments; DR conducted the bioassay experiments; MT conducted the soil chemical and microbiological analysis, TFD analyzed the data; and CB, CG, CW, MA and TFD wrote the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2019.103482.

References

Bonanomi, G., Antignani, V., Capodilupo, M., Scala, F., 2010. Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. Soil Biol. Biochem. 42, 136–144.

Burgess, T.I., Scott, J.K., Mcdougall, K.L., Stukely, M.J., Crane, C., Dunstan, W.A., Brigg, F., Andjic, V., White, D., Rudman, T., 2017. Current and projected global distribution of Phytophthora cinnamomi, one of the world's worst plant pathogens. Glob. Change Biol. 23, 1661–1674.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference - A Practical Information-Theoretic Approach. Springer, New York.

Campos, S.B., Lisboa, B.B., Camargo, F.A., Bayer, C., Sczyrba, A., Dirksen, P., Albersmeier, A., Kalinowski, J., Beneduzi, A., Costa, P.B., 2016. Soil suppressiveness and its relations with the microbial community in a Brazilian subtropical agroecosystem under different management systems. Soil Biol. Biochem. 96, 191–197.

Chakraborty, S., Pangga, I.B., Roper, M.M., 2012. Climate change and multitrophic interactions in soil: the primacy of plants and functional domains. Glob. Change Biol. 18, 2111–2125.

Dawson, T.P., Perryman, A.H., Osborne, T.M., 2016. Modelling impacts of climate change on global food security. Clim. Chang. 134, 429–440.

Döring, T.F., 2015. Grain legume cropping systems in temperate climates. In: De Ron, A. (Ed.), Grain Legumes - Handbook of Plant Breeding. Springer, New York, Heidelberg, pp. 401–434.

Ellmer, F., Baumecker, M., 2005. Static nutrient depletion experiment Thyrow. Results after 65 experimental years. Arch. Agron. Soil Sci. 51, 151–161.

Finckh, M.R., Yli-Mattila, T., Nykönen, A., Kurki, P., Hannukkala, A., 2015. Organic temperate legume disease management. In: Finckh, M.R., van Bruggen, A.H.C., Tamm, L. (Eds.), Plant Diseases and Their Management in Organic Agriculture. APS Press, St. Paul, Minnesota, pp. 293–310.

Geisseler, D., Scow, K.M., 2014. Long-term effects of mineral fertilizers on soil microorganisms – a review. Soil Biol. Biochem. 75, 54–63.

Gómez Expósito, R., de Bruijn, I., Postma, J., Raaijmakers, J.M., 2017. Current insights into the role of rhizosphere bacteria in disease suppressive soils. Frontiers in Microbiol. 8, 2529.

Gregory, A.S., Watts, C.W., Griffiths, B.S., Hallett, P.D., Kuan, H.L., Whitmore, A.P., 2009. The effect of long-term soil management on the physical and biological resilience of a range of arable and grassland soils in England. Geoderma 153, 172–185.

Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. FEMS Microbio. Rev. 37, 112–129.

Griffiths, B., Bonkowski, M., Roy, J., Ritz, K., 2001. Functional stability, substrate utilisation and biological indicators of soils following environmental impacts. Appl. Soil Ecol. 16, 49–61.
Hagn, A., Engel, M., Kleikamp, B., Munch, J.C., Schloter, M., Bruns, C., 2008. Microbial community shifts in *Pythium ultimum*-inoculated suppressive substrates. Biol. Fert. Soils 44, 481–490.
Heijnen, C., Van Veen, J., 1991. A determination of protective microhabitats for bacteria introduced into soil. FEMS Microbiol. Ecol. 8, 73–80.
Jambhulkar, P.P., Sharma, M., Lakshman, D., Sharma, P., 2015. Natural Mechanisms of Soil Suppressiveness Against Diseases Caused by Fusarium, Rhizoctonia, Pythium, and Phytophthora, Organic Amendments and Soil Suppressiveness in Plant Disease Management. Springer, pp. 95–123.
Kuan, H.L., Hallett, P.D., Griffiths, B.S., Gregory, A.S., Watts, C.W., Whitmore, A.P., 2007. The biological and physical stability and resilience of a selection of Scottish soils to stresses. Eur. J. Soil Sci. 58, 811–821.
Kwak, Y.-S., Weller, D.M., 2013. Take-all of wheat and natural disease suppression: a review. The Plant Pathology Journal 29, 125.
Lazányi, J., 2000. Sustainable rye production in the Westsik crop rotation experiment. Acta Agronomica Hungarica 48, 271–277.
Le, C., Hoang, T., Thai, T., Tran, T., Phan, T., Raaijmakers, J., 2018. Isolation, characterization and comparative analysis of plant-associated bacteria for suppression of soil-borne diseases of field-grown groundnut in Vietnam. Biol. Control 121, 256–262.
Löbmann, M.T., Vetukuri, R.R., de Zinger, L., Alsanius, B.W., Grenville-Briggs, L.J., Walter, A.J., 2016. The occurrence of pathogen suppressive soils in Sweden in relation to soil biota, soil properties, and farming practices. Appl. Soil Ecol. 107, 57–65.
Martin, F., Hancock, J., 1986. Association of chemical and biological factors in soils suppressive to *Pythium ultimum*. Phytopath. 76, 1221–1231.
Marzano, S.-Y.-L., Villamil, M.B., Wander, M.M., Ugarte, C.M., Wen, L., Eastburn, D.M., 2015. Organic transition effects on soilborne diseases of soybean and populations of Pseudomonadaceae. Agron. J. 107, 1087–1097.
Mazzola, M., 2002. Mechanisms of natural soil suppressiveness to soilborne diseases. Antonie Van Leeuwenhoek 81, 557–564.
Mazzola, M., 2007. Manipulation of rhizosphere bacterial communities to induce suppressive soils. J. Nematol. 39, 213.
Mendes, R., Kruijt, M., De Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J.H., Piceno, Y.M., DeSantis, T.Z., Andersen, G.L., Bakker, P.A., 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 1203980.
Okubara, P.A., Dickman, M.B., Blechl, A.E., 2014. Molecular and genetic aspects of controlling the soilborne necrotrophic pathogens Rhizoctonia and Pythium. Plant Sci. 228, 61–70.
Pane, C., Spaccini, R., Piccolo, A., Celano, G., Zaccardelli, M., 2019. Disease suppressiveness of agricultural greenwaste composts as related to chemical and bio-based properties shaped by different on-farm composting methods. Biol. Control 137, 104026.
Pautasso, M., Döring, T.F., Garbelotto, M., Pellis, L., Jeger, M.J., 2012. Impacts of climate change on plant diseases – opinions and trends. Eur. J. Plant Pathol. 133, 295–313.
Pflughöft, O., 2008. Pilzkrankheiten in Körnerfuttererbsen (*Pisum sativum* L.) – Diagnose, Epidemiologie, Ertragsrelevanz und Bekämpfung, Faculty of Agricultural Sciences. University of Göttingen, Germany.
Ramier, D., Boulain, N., Cappelaere, B., Timouk, F., Rabanit, M., Lloyd, C.R., Boubkraoui, S., Métayer, F., Descroix, L., Wawrzyniak, V., 2009. Towards an understanding of coupled physical and biological processes in the cultivated Sahel–1. Energy and water. J. Hydrol. 375, 204–216.
Reckling, M., Bergkvist, G., Watson, C.A., Stoddard, F.L., Zander, P.M., Walker, R.L., Pristeri, A., Toncea, I., Bachinger, J., 2016. Trade-offs between economic and environmental impacts of introducing legumes into cropping systems. Front. Plant Sci. 7, 669.
Saeed, M.F., Baćanović, J., Bruns, C., Schmidt, H., Finckh, M.R., 2017. Seed health of organic peas and faba beans and its effects on the health of the harvested grains. Journal of Plant Diseases and Protection 124, 331–337.
Schroeder, K., Okubara, P., Tambong, J., Lévesque, C., Paulitz, T., 2006. Identification and quantification of pathogenic Pythium spp. from soils in eastern Washington using real-time polymerase chain reaction. Phytopath 96, 637–647.
Seethapathy, P., Kurusamy, R., Kuppusamy, P., 2017. Soil borne diseases of major pulses and their biological management. Innovative Farming 2, 1–11.
Tamm, L., Thürig, B., Bruns, C., Fuchs, J.G., Köpke, U., Laustela, M., Leifert, C., Mahlberg, N., Nietlispach, B., Schmidt, C., 2010. Soil type, management history, and soil amendments influence the development of soil-borne (*Rhizoctonia solani*, *Pythium ultimum*) and air-borne (*Phytophthora infestans*, *Hyaloperonospora parasitica*) diseases. Eur. J. Plant Pathol. 127, 465–481.
Termorshuizen, A.J., van Rijn, E., vander Gaag, D.J., Alabouvette, C., Chen, Y., Lagerlöf, J., Malandrakis, A.A., Paplomatas, E.J., Rämert, B., Ryckeboer, J., Steinberg, C., Zmora-Nahum, S., 2006. Suppressiveness of 18 composts against 7 pathosystems: variability in pathogen response. Soil Biol. Biochem. 38, 2461–2477.
Thompson, S.E., Levin, S., Rodriguez-Iturbe, I., 2014. Rainfall and temperatures changes have confounding impacts on *Phytophthora cinnamomi* occurrence risk in the southwestern USA under climate change scenarios. Glob. Change Biol. 20, 1299–1312.
van Toor, R., Chng, S., Warren, R., Butler, R., Cromey, M., Craigie, R., McCloy, B., 2016. Wheat cultivar susceptibility to *Gaeumannomyces graminis* var. *tritici* and influence on Pseudomonas fluorescence numbers in the rhizosphere. Australasian Plant Path. 45, 595–607.
van der Voort, M., Kempenaar, M., van Driel, M., Raaijmakers, J.M., Mendes, R., 2016. Impact of soil heat on reassembly of bacterial communities in the rhizosphere microbiome and plant disease suppression. Ecol. Lett. 19, 375–382.
Walker, R., Edwards, A., Watson, C.A., Campbell, C., Hillier, S., Morrice, L., 2010. Nutrient Cycling and Soil Fertility Information Gained From Various Long-term Field Experiments Established on a Granitic Derived Soil Located in NE Scotland.
Walker, R.L., Edwards, A.C., Watson, C.A., 2014. Nutrient input and climatic effects on the dry biomass productivity of a crop rotation over 60 years. In: European Society of Agronomy XIIIth Congress. Debrecen University, Debrecen.
Watson, C., Baddeley, J., Edwards, A., Rees, R., Walker, R., Topp, C., 2011. Influence of ley duration on the yield and quality of the subsequent cereal crop (spring oats) in an organically managed long-term crop rotation experiment. Organic Agr. 1, 147.
Watson, C.A., Topp, C.F.E., Walker, R.L, 2015. Long-term productivity of legume based crop rotations. Asp. Appl. Biol. 128, 189–194.
Watson, C.A., Reckling, M., Preissel, S., Bachinger, J., Bergkvist, G., Kuhlman, T., Lindström, K., Nemecek, T., Topp, C.F., Vanhatalo, A., 2017. Grain legume production and use in European agricultural systems. In: Adv. Agron. Elsevier, pp. 235–303.
Weller, D.M., Raaijmakers, J.M., Gardener, B.B.M., Thomashow, L.S., 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu. Rev. Phytopathol. 40, 309–348.
Wertz, S., Degrange, V., Prosser, J.I., Poly, F., Commeaux, C., Guillaumaud, N., Le Roux, X., 2007. Decline of soil microbial diversity does not influence the resistance and resilience of key soil microbial functional groups following a model disturbance. Envir. Microbiol. 9, 2211–2219.
Wiebe, K., Lotze-Campen, H., Sands, R., Tabeau, A., van der Mensbrugghe, D., Biewald, A., Bodirsky, B., Islam, S., Kavallari, A., Mason-D'Croz, D., 2015. Climate change impacts on agriculture in 2050 under a range of plausible socioeconomic and emissions scenarios. Environ. Res. Lett. 10, 085010.