Eur J Plant Pathol (2010) 127:465–481
DOI 10.1007/s10658-010-9612-2

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

Lucius Tamm · Barbara Thürig · Christian Bruns · Jacques G. Fuchs · Ulrich Köpke · Matias Laustela · Carlo Leifert · Nicole Mahlberg · Bruno Nietlispach · Christoph Schmidt · Felix Weber · Andreas Fließbach

Accepted: 22 March 2010 / Published online: 24 April 2010

Abstract The impact of soil type, long-term soil management, and short-term fertility input strategies on the suppressiveness of soils against soil-borne (*Ocimum basilicum – Rhizoctonia solani*, *Lepidium sativum – Pythium ultimum*) as well as air-borne (*Lycopersicon esculentum – Phytophthora infestans*, *Arabidopsis thaliana – Hyaloperonospora parasitica*) diseases was studied. Soils from field trials established in five European sites with contrasting pedo-climatic conditions were examined. Sites included (i) a long-term management field trial comparing organic and conventional farming systems (DOK-trial, Therwil, Switzerland) (ii) a short-term fertility input field trial comparing mineral and organic matter fertilisation regimes (Bonn (BON), Germany) (iii) two short-term fertility input field trials (Stockbridge (STC) and Tadcaster (TAD), UK) comparing the impact of farmyard manure, composted farmyard manure, and chicken manure pellet amendements and (iv) soil from a site used as a reference (Reckenholz (REC), Switzerland). Soil type affected disease suppressiveness of the four pathosystems signficantly, indicating that soils can not only affect the development of soil-borne, but also the resistance of plants to air-borne diseases at relevant levels. Suppressiveness to soil- and air-borne diseases was shown to be affected by soil type, but also by long-term management as well as short-term fertility inputs.

Keywords *Ocimum basilicum* · *Lepidium sativum* · *Lycopersicon esculentum* · *Arabidopsis thaliana* · Soil characteristics

Lucius Tamm and Barbara Thürig contributed equally to the publication.

L. Tamm (✉) · B. Thürig · J. G. Fuchs · M. Laustela · N. Mahlberg · B. Nietlispach · F. Weber · A. Fließbach
Research Institute of Organic Agriculture (FiBL),
5070 Frick, Switzerland
e-mail: lucius.tamm@fibl.org

M. Laustela
e-mail: matias.laustela@friedlipartner.ch

C. Bruns
University of Kassel,
37213 Witzenhausen, Germany

C. Leifert · C. Schmidt
Nafferton Ecological Farming Group (NEFG),
University of Newcastle,
Newcastle-upon-Tyne NE43 7XD, UK

U. Köpke
Institute of Organic Agriculture, University of Bonn,
53115 Bonn, Germany

Present Address:
M. Laustela
FriedliPartner AG,
Baumackerstrasse 24,
8050 Zürich, Switzerland

Introduction

One of the principles of organic farming is to attain ecological balance through the design of farming systems, establishment of habitats and maintenance of diversity. Inputs should be reduced in order to maintain and improve environmental quality and conserve resources (Tamm 2001). However, there are still some 'technological' bottlenecks in organic production systems which potentially affect quality and safety in organic foods, the environment, as well as costs of production. These bottlenecks include insufficient and/or untimely availability of nutrients as well as occurrence of pests and diseases (Tamm 2001). One approach to overcome such bottlenecks is the improvement of soil properties by agricultural practices such as soil tillage, crop rotation or the application of organic amendments. Agricultural practices not only have an obvious and direct impact on plants by affecting soil parameters such as erosion stability, nutrient availability and water holding capacity, but also an indirect effect by affecting soil organisms and their activities (Govaerts et al. 2007; Rotenberg et al. 2007; Van Elsas et al. 2002). An active and abundant soil flora and fauna is thought to improve soil fertility and quality parameters (Doran et al. 1996). Rapid mineralisation of mineral nutrients from organic matter in synchrony with plant demand is of crucial importance in organic agriculture, where only organic fertilisers can be used. In addition, soil (micro)organisms have been shown to be a key factor in the suppression of soil-borne diseases (Knudsen et al. 2002; Menzies 1959; Shipton et al. 1973; Stutz et al. 1986; Wiseman et al. 1996). Mechanisms involved in suppression of soil-borne diseases by soil microorganisms have been extensively studied and include competition for nutrients and space, antibiosis, hyperparasitism and the induction of plant disease resistance (Haas and Défago 2005; Hoitink et al. 1977; Theodore and Toribio 1995). Some studies have demonstrated that soil microorganisms may also reduce disease development of air-borne, foliar diseases (van Loon et al. 1998). Here, beneficial microorganisms and pathogens are physically separated, and induced systemic resistance (ISR) has been identified as the main underlying mechanism (van Loon and Bakker 2005). The occurrence of ISR against air-borne diseases has been demonstrated mainly in controlled conditions, while little is known about the occurrence and relevance of this phenomenon under field conditions (Kloepper et al. 1999). Organic matter amendments (e.g. manure, compost, plant residues) to soil were shown to affect soil microbial populations and soil suppressiveness by (i) promoting beneficial microorganisms native to the soils and/or (ii) by introduction of new beneficial microorganisms (Chu et al. 2007; Inbar et al. 2005; Innerebner et al. 2006; Pérez-Piqueres et al. 2006; Serra-Wittling et al. 1996; Van Elsas et al. 2002). Organic farming systems using regular organic matter amendments have been shown to have higher microbial biomass and activity compared to conventional farming systems using mineral fertilisers only (Bossio et al. 1998; Mäder et al. 2002). However, other studies suggest that soil type and not soil management is the main determinant for soil microbial activity and community structure (Garbeva et al. 2004).

In a pilot study in 2000, the impact of soil properties on plant diseases was assessed. This study aimed at assessing the variability of inherent suppressiveness to soil-borne and air-borne diseases in soils from commercial organic farms by comparing soils from 15 potato fields in Switzerland, which were sampled immediately before planting. The bioassays tomato-*Phytophthora infestans* and cucumber-*Pythium ultimum* were selected as test systems to assess suppressiveness to air-borne or soil-borne diseases respectively. In this empiric study, positive correlations between disease suppressiveness and parameters which describe soil microbial biomass and activity (C_{mic}, basal respiration), but also correlations between suppressiveness and macro-/micronutrients were found (Berner et al. 2002). This pilot study therefore indicated that (i) there are differences in suppressiveness not only to soil-borne but also to air-borne diseases in commercial farming practice and (ii) suppressiveness can be quantified by bioassays. However, causal relationships between soil properties and suppressiveness could not be identified and the relative importance of site-specific as opposed to cultivation-mediated parameters remained unknown.

In the study reported here, the main aim was to quantify the relative importance of site-specific *vs.* cultivation-mediated soil properties for soil suppressiveness towards soil-borne and foliar diseases. A total of four field sites with established factorial trials focused on comparing different soil fertility management regimes were selected in Switzerland, Germany

and the UK in order to quantify the effect of (i) site-specific soil characteristics, (ii) long-term farming practices, and (iii) short-term fertilisation regimes on soil suppressiveness. Soil samples were submitted to soil analyses (physical, chemical, and microbiological) and assessed for suppressive properties by two bio-assays for soil-borne (*Ocimum basilicum* - *Rhizoctonia solani*, *Lepidium sativum* - *Pythium ultimum*) and two for air-borne foliar diseases (*Lycopersicon esculentum* - *Phytophthora infestans*, *Arabidopsis thaliana* – *Hyaloperonospora parasitica*).

Materials and methods

Field trials

DOK Long-term farming systems comparison trial To assess the impact of long-term management, soil samples from a long-term, replicated Swiss farming-systems-comparison study (DOK-trial) were analysed. In this trial soils were cropped with the same sequence of crops in the rotation, but exposed to different organic and conventional management systems since 1978 (Mäder et al. 2002, 2006). Biodynamic (BIODYN), bio-organic (BIOORG) and conventional (CONFYM) farming systems are compared in a replicated (n=4) 7-year rotation experiment at 2 fertility input regimes (manure/composted manure inputs equivalent to 0.7 and 1.4 livestock units (LSU) per hectare) (Table 1). The CONFYM plots are fertilized with manure at the same fertility input level as the organic systems and they receive additional mineral fertilizers as recommended according to Swiss integrated farming procedures. The BIOORG system uses manure and the BIODYN system uses composted manure at the same organic matter input level. Two sets of control plots are included in the trial, an unfertilized control (NOFERT) and a conventional control (CONMIN) which mimics a stockless conventional system where only mineral fertilizers are used. As a result, a range of soils with significantly different soil characteristics (e.g. soil biological activity is 50 to 100% higher in organic compared to conventional soils) have developed from the same original soil type (Mäder et al. 2002). Soil samples from this trial were used to study the long-term effect of organic matter based fertility inputs on soil physical, chemical and biological characteristics.

Short-term fertility-input trials Short-term fertility-input field trials were set up in spring 2004 on the organic research farm 'Wiesengut' in North-Rhine Westphalia (Germany) (BON), at the Stockbridge Technology Center (STC) in Yorkshire (UK) and at a commercial organic farm in Tadcaster (TAD) in Yorkshire (UK). All experiments were designed as fully factorial randomized block designs with four replications. In BON, treatments included fresh farmyard manure (FYM), composted FYM and a mineral fertilizer (calcium ammonium nitrate, MIN) at two fertiliser input levels (85 and 170 kg N ha^{-1}) (Table 1). In STC and TAD, treatments included composted FYM (from Nafferton Farm, Newcastle, UK, 1.18% N), chicken manure pellets (commercial product, Greenvale, Yorkshire, UK, 4.4% N) and a mix of chicken manure and composted FYM at one fertiliser input level (170 kg N ha^{-1}).

Sampling of soils In the DOK-trial, a representative pooled sample from the four replicate field plots and the three crops (grass-clover 2nd yr, catch crops before maize and soybeans) was taken from each farming system separately in March 2004. For the bioassay *A. thaliana – H. parasitica*, soil samples were taken again in April 2005 from plots planted with the intercrop fodder rye after soy bean. At this time samples of all four field replicates from five treatments were taken and kept separate. In all short-term field trials, one set of soil samples were taken before fertility inputs (abbreviated as **B**efore **F**ertility **I**nput BFI) in spring 2004. Another set of soil samples was taken after application of soil fertility inputs and the planting of lettuce (BON) or onions (STC, TAD) when the crops reached maximum vegetative growth rates (abbreviated as **A**fter **F**ertility **I**nput AFI). AFI-samples were taken in July (BON) or in October (STC, TAD) 2004 respectively. In addition, samples for a reference soil (a soil that was frequently used in previous experiments; REC) was taken in June 2005 after harvest of wheat.

Soils were sampled randomly with a 3 cm soil corer from the 0–20 cm soil layer in each field plot. Soil samples were homogenised, sieved at 2 mm mesh size for soil analyses and 8 mm for bioassays and stored at 2–4°C in the dark at approx 50% water holding capacity until soil analyses and bioassays were conducted.

Table 1 Summary of treatments and rates of application in field experiments

	DOK (CH)	BON (DE)	TAD (UK)	STC (UK)	REC (CH) (reference soil)
Coordinates	47°30′N; 7°33′E	50°48′ N; 7°17′ E	53°53′N;−1° 16′ W	53°28′N, 1°36′W	47°28′N, 8°54′E
Soil type	haplic luvisol	fluvisol	calcic cambisol	gleysol	eutric cambisol
Sand/silt/clay [a]	8/78/14	50/38/12	48/30/22	86/6/8	63/15/22
pH [a]	5.63	6.70	7.24	7.01	7.41
C_{org} (mg g^{-1}) [a]	14.03	11.05	29.90	16.96	19.9
Sampling date BFI [c]	–	20.04.2004	05.05.2004		
Sampling date AFI [d]	17.03.2004/ 5.4.2005	06.07.2004	15.10.2004		June 2005
Strategies	No fertilizer (NOFERT)	Farmyard manure (FYM)	Composted FYM (CompFYM)		
	Mineral fertilizer (CONMIN) 2	Composted FYM (CompFYM)	Chicken manure (ChickMan)		
	Biodynmaic 1&2 (BIODYN)	Mineral fertilizer (MIN)	Mixed ChickMan and CompFYM (ChickMan + CompFYM)		
	Bioorganic 1&2 (BIOORG)				
	Integrated 1&2 (CONFYM)				
Intensities	1: 0.7 LSU [b]	85 kg N ha^{-1}	170 kg N ha^{-1}	170 kg N ha^{-1}	
	2: 1.4 LSU [b]	170 kg N ha^{-1}			
	3 crops pooled	Lettuce	Onion		
Samples	8	8 BFI[c] +24 AFI[d]	4 BFI[c] +12 AFI[d]	4 BFI[c] +12 AFI[d]	
Replicates	0	4	4	4	

[a] average values of all treatments; [b] LSU: livestock units ha^{-1} yr^{-1} ; [c] before fertility input; [d] after fertility input

Soil analyses

Particle size distribution was analysed according to standard procedures (Blume et al. 2000) in soils of the DOK farming systems and in all BFI samples of the short-term trials. Soil aggregate stability was analysed by wet sieving according to Kandeler (Kandeler 1993), cation exchange capacity was determined according to ISO 13536 at pH 8.1, pH was determined in a soil suspension water 1:5 (weight/vol), total organic carbon and nitrogen were determined in a CHN analyzer (LECO, St. Joseph, Michigan, US) and inorganic carbon was determined as the difference after acidification. Mineral nitrogen was analysed in soil samples extracted directly after sampling or in frozen samples after extraction with1:4 (w/vol) 0.01 M $CaCl_2$. Phosphorus and potassium were extracted with CAL (calcium acetate and calcium lactate) for determination of total soil P and K content. Soluble fractions of P, K, S, Ca, Mg, Na, Cu, Zn, Mn, Fe, B, Mo, Al, Cd, Ni, Pb were determined by inductively coupled argon plasma optical emission spectrometry (Varian) after soil extraction according to Mehlich (Mehlich 1984).

Soil microbial biomass was determined by a chloroform fumigation extraction assay according to (Brookes et al. 1985; Vance et al. 1987) and by measuring extracted carbon and nitrogen after combustion at 850°C by infrared spectrometry and chemoluminescence respectively (Dimatec Essen, Germany). Soil basal respiration was measured by titration of trapped CO_2 in alkali (Jäggi 1976) and also as O_2 consumption using the Sensomat system (Aqualytic, D). Soil enzyme activities (alkaline phosphatase activity, protease activity, dehydrogenase activity, and FDA hydrolysis) were determined according to the procedures described in Alef and Nannipieri (Alef and Nannipieri 1995).

Bioassays

Lepidium sativum L. – *Pythium ultimum*: Untreated organic seeds of the *L. sativum* variety ‘Einfache Kresse’ from Eric Schweizer Samen AG, CH-Thun were used. Inoculum of *P. ultimum* (kindly provided by Syngenta, CH-Stein) was produced on a millet medium (24 g sterile millet + 20 ml H_2O demin). After ten days of incubation at 20°C, the mycelium together with the millet seeds were homogenized by an onion chopper before use. All soils under investigation were amended with 10 g of a sand / *P. ultimum* / millet seed inoculum mixture, previously adjusted to a final density of 0, 0.25, 1, 2, 4 g of *P. ultimum* /millet seed per l of soil. Inoculum densities of 16 and 64 g l^{-1} were created by directly amending soils and substrates with the *P. ultimum* / millet seed inoculum. No fertilizer was applied to the test soils. The experimental setup included a total of 6 dosages of active *P. ultimum* inoculum (0, 0.25, 1, 2, 4, 16, 64 g l^{-1} soil or growth substrate) and 5 replicates per *P. ultimum* inoculum concentration. Inoculated substrates were pre-incubated in plastic containers with a perforated lid at 20°C in the dark for 2 days. Pots (Ø 6 cm, 95 ml) were filled with soil and then sown with 0.5 g seeds of *Lepidium sativum* (untreated organic seeds, Eric Schweizer Samen AG, CH-Thun) each. Subsequently, pots were placed on individual plates in order to avoid cross-contamination between treatments. Within a replicate, pots were completely randomised, and incubated in growth chambers at 23°C (day) and 18°C (night) with a day-length of 16 h for 2 days. For the first two days, pots were covered with transparent plastic bags to ensure 100% relative humidity for germination. Shoot fresh weight was assessed 7 days after sowing, before the first true leaves started to appear. Shoot fresh weight is a good measure for the overall effect of *P. ultimum* on *L. sativum*, which is a combination of pre-emergence damping-off and inhibition of growth of germinated *L. sativum* plants. Weight reduction caused by *P. ultimum* was calculated for each pot as 100 * (a * b^{-1}), where a = shoot weight in pots inoculated with *P. ultimum*, b = mean shoot weight in control pots.

Ocimum basilicum L – *Rhizoctonia solani*: Untreated organic seeds of the variety ‘Common basil’ from Eric Schweizer Samen AG, CH-Thun were used. Inoculum of *R. solani* (kindly provided by Syngenta, CH-Stein) was produced on a millet medium (sterile 25 g millet + 15 ml H_2Odemin). After 2 weeks of incubation at 20°C, the mycelium together with the millet seeds were homogenized by an onion chopper before use. Pots with a volume of 285 ml were amended with a total of 1 g of a *R. solani*/millet seed/sand mixture adjusted to 4 concentrations of *R. solani*/millet seed inoculum (0, 88, 352 and 704 mg per liter soil). Six replicates per inoculum dosage were used. The *R. solani*/millet seed/sand-inoculum mixture was placed in a layer in the test

soils at 10 cm depth. Seeds of basil (*O. basilicum*) were planted and covered with 20 ml vermiculite per pot. Subsequently, pots were carefully watered and covered with transparent plastic bags during 4 days to ensure 100% relative air humidity and incubated at 18–25°C and 16 h light. Fresh weight of shoots was assessed 14 d after planting. Weight reduction caused by *R. solani* was calculated for each pot as 100 * (a * b^{-1}), with a = shoot weight in pots inoculated with *R. solani*, b = mean shoot weight in control pots.

Arabidopsis thaliana L. – *Hyaloperonospora parasitica*: *A. thaliana* plants ecotype Columbia (*Col-0*) were cultivated in pots filled with 80 ml of soil in a growth chamber with a 10 h day (100–120 μE m^{-2} s^{-1} at 23°C) and 14 h night (18°C) cycle at 70% relative air humidity. Plants were thinned to 3 plants per pot one week after sowing. Plants were fertilized weekly with a mineral fertilizer (Hauert-Flory ® 3/type A, PLANTA Düngemittel GmbH, D-Regenstauf) at a concentration of 0.125 g l^{-1} soil in order to ensure optimal plant nutrition. Plants were grown under the conditions described above for 21 days and then inoculated with *H. parasitica* strain NOCO (20,000 sporangia ml^{-1}) using a chromatography sprayer. Inoculated plants were incubated at 20°C, 100% relative air humidity with a 10 h light and 14 h night cycle. Subsequently, relative humidity was reduced to 80% for 5 d and then increased again to 100% to induce sporulation before scoring. Disease severity (percentage leaf area covered by sporangiophores) was assessed for each plant separately on both the upper and lower side of leaves. The experimental setup included 12 replicates per treatment, each replicate representing the mean of three individual plants.

Lycopersicon esculentum Mill. – *Phytophthora infestans*: Untreated organic seeds of the tomato variety 'Roter Gnom' were used (kindly provided by Syngenta AG, CH-Stein). Tomato plants were grown in the greenhouse at a temperature of 20–25°C under natural light. In winter time and at low light intensities the light intensity was increased by lamps (250 W/D, 12–15 kLux) and extended to a day period to 16 h. Until emergence of the first true leaves, tomato plants were cultivated on a vermiculite – substrate mixture (91% (v/v) vermiculite, 9% 'Einheitserde Typ 0'(Gebr. Patzer GmbH & Co. KG, D-Sinntal-Jossa) amended with stone meal (1.53 g l^{-1} substrate)), watered to saturation with a solution containing 2 g l^{-1} of Hauert-Flory ® 3/type A. After two weeks, seedlings were transplanted to individual pots containing 750 ml of test soil. Plants were fertilized once a week with a mineral fertilizer (0.13 g l^{-1} soil Hauert-Flory ® 3/type A) in order to ensure optimum plant nutrition. Tomato plants were watered to field capacity (measured by conductivity sensors) by drip irrigation with an automatic watering system. At the growth stage of 5–8 fully expanded leaves, plants were transferred to growth chambers (16 h light, 18°C, 70–90% relative air humidity) for inoculation with *P. infestans* (kindly provided by Syngenta, CH-Stein). The sporangia were harvested from 2 week old cultures cultivated on rye agar (1 l rye brew (boil 200 g organic rye in 1 l water for 1 h), 5 g l^{-1} glucose, 20 g l^{-1} agar). Sporangia suspensions (40,000 sporangia ml^{-1}) were incubated for 2 h at 0°C before inoculation. Tomato plants were covered with a transparent hood two hours before inoculation. Drops of 5 μl of the innoculum suspension were applied on the 3 apical leaflets of 4 true leaves of the plants, resulting in a total of 12 inoculations per plant. After inoculation, plants were covered again with a transparent hood and incubated at 100% RH for 48 h at 18°C and subsequently, after removal of hoods, incubated (16 h light 5 kLux, 18°C, 70–90% relative air humidity) for 5 days. Disease development was assessed 7 days post inoculation by measuring the lesion diameter of each individual inoculation site. Soils from each field sample were pooled after the bioassay, homogenised and tested again as described above ('recycled soils'), except in the experiment designed to test for site effects. Six or five (recycled soils) pots respectively represented each field sample.

Statistical analysis

Results were analysed by two factor ANOVA with experimental set and treatment as factors. In case of significant model effects, a posthoc Tukey-B test was applied to test for differences between individual treatments at $p=0.05$ (SPSS 13.0). Soil characteristics were examined by principal component analysis (PCA) (CANOCO, Biometris, Plant Research International, Wageningen UR, NL). For figures, disease data of the two bioassays with air-borne diseases were standardized as follows: standardized disease=a * b^{-1}, with a = disease $sample_x$ and b = mean disease whole experiment.

Results

Soil type (site)

Principal component analysis of soil physical, chemical and microbiological parameters detected a clear differentiation of the soils from the four field sites under examination (Fig. 1). Soil parameters contributing most to this differentiation include physical (sand and silt content) (Table 2), chemical (cation exchange capacity, content of micro-nutrients (Ca, Mg, Cu, B, Pb)) and total soil carbon (C_{tot}) and nitrogen (N_{tot}) as well as the biological parameters (fluorescein diacetate hydrolysis, alkaline phosphatase activity, basal respiration).

In both bioassays for soil-borne diseases, different dosages of the disease did not result in dose-effect curves (Fig. 2). Therefore, results of pots amended with different dosages of the pathogen were pooled in subsequent analyses.

Site had a significant effect on the development of soil-borne as well as air-borne diseases (Fig. 3). In the

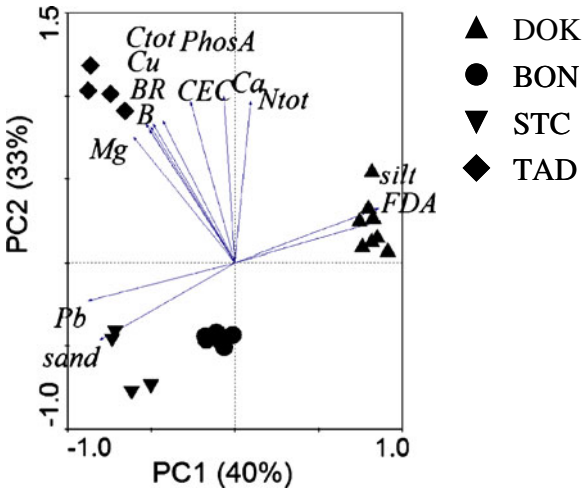

Fig. 1 Ordination of the first two ordination axes as determined by principal component analysis (PCA) of soil physical, chemical and biological parameters of before fertility input samples from sites Stocksbridge (STC), Tadcaster (TAD) and Bonn (BON) and the DOK-samples. The percentage of explained variance is displayed in parentheses along the first two ordination axes. Arrows show parameters contributing most to the first principal components (species fit >90%). *BR* basal respiration, *CEC* cation exchange capacity, *Ctot* total carbon, *DHA* dehydrogenase activity, *FDA* fluorecein diacetate hydrolysis, *Ktot* total K, *Ntot* total nitrogen; *PhosA* alkaline phosphatase activity

Table 2 Physical parameters of soils under examination. For abbreviations of treatments see Table 1

Site	Microaggregate stability %	Macroaggregate stability%	Sand %	Silt %	Clay %
DOK	34	36	15	70	15
BON	34	67	50	38	12
STC	25	40	86	6	8
TAD	34	55	48	30	22

bioassays *A. thaliana – H. parasitica* and *L. sativum* - *P. ultimum*, plants developed lowest disease levels if grown on soil STC, highest disease levels if grown in soils from the DOK trial, and intermediate disease levels if grown on the reference soil REC. In contrast, *L. esculentum* plants were most susceptible to *P. infestans* if grown on soil REC. In the bioassay *O. basilicum – R. solani*, addition of *R. solani* reduced fresh weight of *O. basilicum* most on soils TAD, STC and BON and least on soil REC. Fresh weight of *O. basilicum* without addition of *R. solani* differed strongly between soils, with highest weights on soils STC and REC, intermediate weights on soil BON and smallest weights on soils THE and TAD. The impact of soil types on disease development was most pronounced in the bioassay *A. thaliana* - *H. parasitica*, where plants grown on the most suppressive soil (STC) developed on average six times less disease symptoms than plants grown on the least suppressive soil (DOK). The bioassay *L. sativum* -*P. ultimum* was less sensitive, with significant weight reductions caused by *P. ultimum* between −24% (BON) and −58% (DOK). In the bioassay *L. esculentum – P. infestans*, differences between least and most suppressive soil were smallest but in some cases significant, with differences around 20%.

Long-term management

Principal component analysis on soil parameters indicates a differentiation of soil parameters between the management strategies (Fig. 4). Soil parameters contributing most to this differentiation included microbial biomass and activity (dehydrogenase activity, alkaline phosphatase activity), macro- (total N, total K) and micronutrients (Mg, B). The three farming systems with low fertility input conventional (CONFYM), bioorganic (BIOORG) and biodynamic (BIODYN)

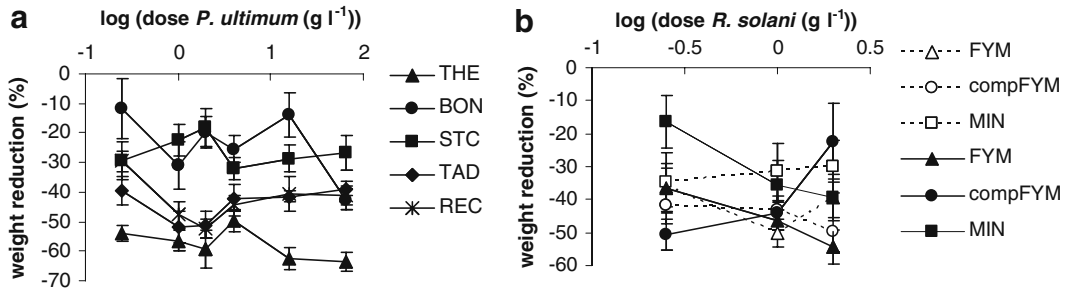

Fig. 2 Examples of dose-response curves in the bioassays *L. sativum* - *P. ultimum* and *O. basilicum* – *R. solani*. **a** Percentage weight reductions caused by dosages of *P. ultimum* in soils from five sites. **b** Percentage weight reductions caused by *R. solani* in 6 different soil amendments at trial site BON. The figure shows means and standard errors (n=6)

formed a cluster in between the two extremes NOFERT and BIODYN at normal fertility input level. All normal fertility input level strategies, including CONMIN, CONFYM, BIODYN and BIO-ORG did not form a cluster but individually separated from NOFERT and all low fertility input level strategies. Differences in soil parameters between management systems detected in this study were similar to those reported in previous studies (Mäder et al. 2002).

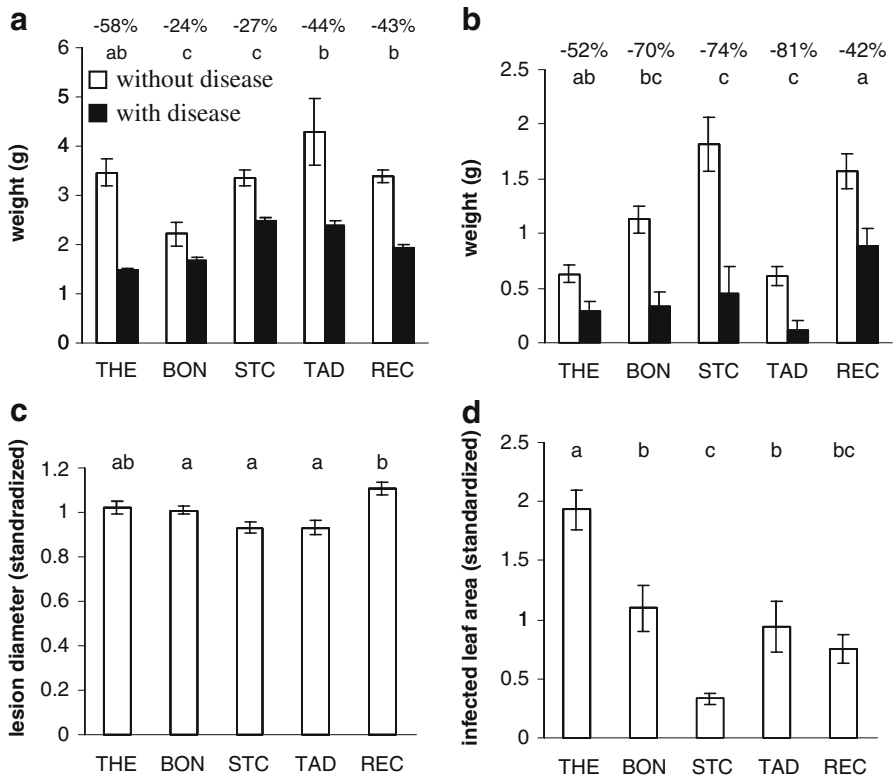

Fig. 3 Effect of soils from five sites on disease development in the bioassays (**a**) *L. sativum* - *P. ultimum*, (**b**) *O. basilicum* - *R. solani* (**c**) *L. esculentum* - *P. infestans* and (**d**) *A. thaliana* - *H. parasitica*. **a** and **b** The figures shows the fresh weight of *L. sativum* or *O. basilicum* shoots respectively in soils not amended (white bars) or amended (black bars) with *P. ultimum* or *R. solani* respectively. Percentages are weight reductions by *P. ultimum* or *R. solani* respectively, letters indicate significant differences in weight reductions (Tukey-B, α=0.05). **b** and **c** The y-axis show the relative diseases calculated as a * b^{-1} with a = disease sample and b = mean disease experiment. The figures show results from one (**a**) two (**b**, **c**) or five (**d**) experiments, bars are means±SE, different letters indicate significant differences (Tukey-B, α=0.05)

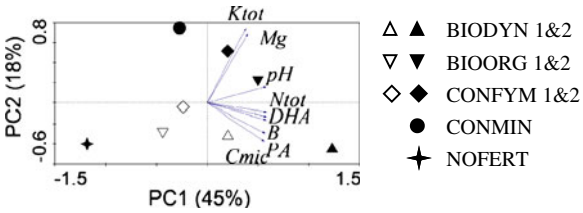

Fig. 4 Ordination of the first two ordination axes as determined by principal component analysis (PCA) of soil chemical and biological parameters of the 8 strategies of the DOK trial. For abbreviations of treatments see Table 1.The percentage of explained variance is displayed in parentheses along the first two ordination axes. Arrows show parameters contributing most to the first principal components (species fit >90%). *B* boron, *DHA* dehydrogenase activity, *Ktot* total K, *Mg* magnesium, *Ntot* total nitrogen, *PA* protease activity

Significant differences in suppressiveness between strategies were found in all four bioassays under study (Fig. 5). However, the extent of suppressiveness depended on the bioassay. (i) In the bioassay *L. esculentum* - *P. infestans*, NOFERT was most suppressive and differed significantly from all other strategies. (ii) *A. thaliana* grown on BIODYN normal fertility input level were least susceptible to *H. parasitica* and differed significantly from CONMIN, CONFYM and BIOORG (all normal fertility input level), while NOFERT showed intermediate suppressiveness, and was significantly different from CONFYM and CONMIN only. (iii) In the bioassay *L. sativum* - *P. ultimum*, at the low fertility input level,

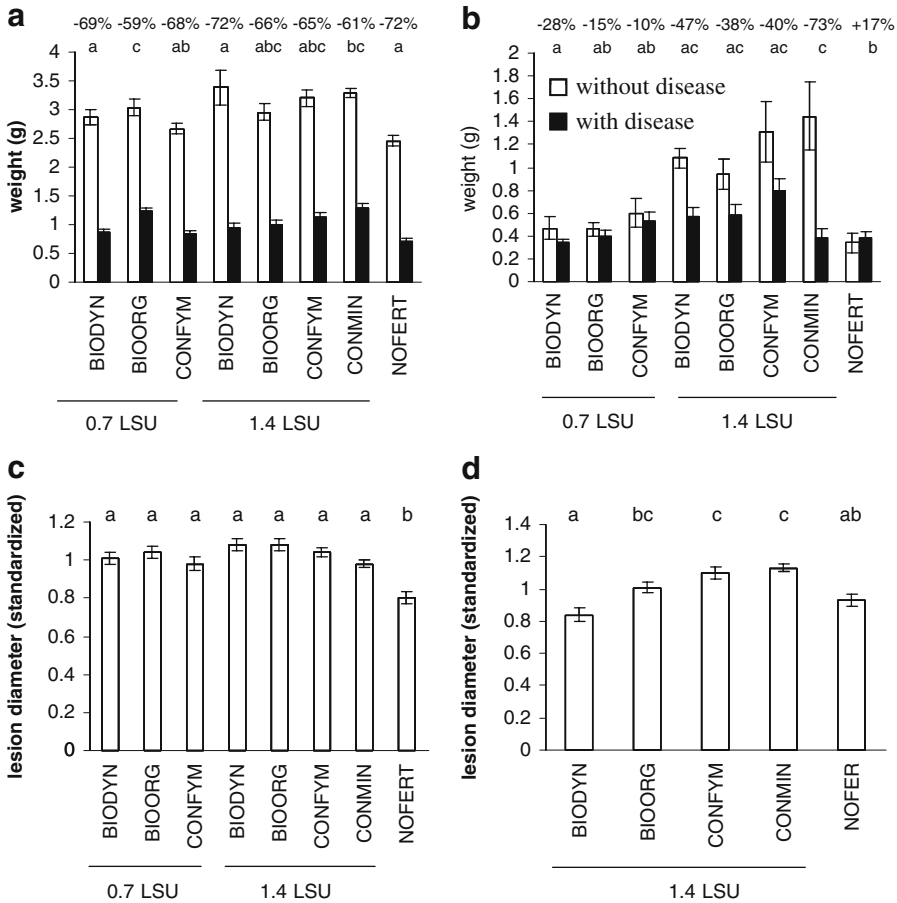

Fig. 5 Effect of long-term management on disease development in the bioassays (**a**) *L. sativum* - *P. ultimum*, (**b**) *O. basilicum* - *R. solani* (**c**) *L. esculentum* - *P. infestans* and (**d**) *A. thaliana* - *H. parasitica*. **a** and **b** The figures show the fresh weight of *L. esculentum* or *O. basilicum* shoots respecitively in soils not amended (white bars) or amended (black bars) with *P. ultimum or R. solani*. Percentages are weight reductions by the diseases, letters indicate significant differences in weight reductions. **b** and **c** The y-axis show the relative diseases calculated as a * b^{-1} with a = disease sample and b = mean disease experiment. The figures show results from one (**a**, **b**, **d**) or two (**c**) experiments, bars are means±SE, different letters indicate significant differences (Tukey-B, α=0.05). For abbreviations of treatments see Table 1

BIOORG was more suppressive than BIODYN and CONFYM and NOFERT. At the high fertility input level, no differences in suppressiveness were found between the strategies obtaining organic fertilizer (CONFYM, BIOORG, BIODYN), whereas the strategy obtaining mineral fertilizer only (CONMIN) was significantly more suppressive than BIODYN and NOFERT. (iv). In the bioassay *O. basilicum* - *R. solani*, nutrient availability limited plant growth. In the absence of *R. solani*, *O. basilicum* growing on the no or low fertility input levels, had a much lower weight than plants growing on normal fertility input level strategies. Inoculation with *R. solani* did not further reduce the weight of *O. basilicum* for the low fertility input level treatments, but reduced the fresh weight of plants growing on normal fertility input level treatments.

Short-term soil amendments

Soil samples taken after the amendment of organic or mineral fertilisers and after culturing onion (trial sites STC and TAD) or lettuce (trial site BON) (AFI) differed from the corresponding before-fertility input (BFI) samples mainly in biological parameters (Tables 3, 4 and 5) but also in some chemical parameters. At trial site BON, AFI samples had lower microbial biomass (C_{mic}, N_{mic}) and microbial activities (basal respiration, protease and dehydrogenase activities) than BFI samples. In contrast, alkaline phosphatase activity was higher in one of the AFI treatments (composted FYM at the high fertility input level) compared to BFI samples. At trial sites TAD and STC, many biological parameters were higher in the AFI as compared to the BFI samples, including basal respiration, qCO_2, alkaline phosphatase and protease activities at site STC as well as C_{mic} and basal respiration at site TAD. Only fluorescein diacetate hydrolysis was lower in the AFI samples at site STC.

The type of amendment had only a small effect on soil parameters (Tables 3, 4 and 5). At site BON, microbial biomass (C_{mic}, N_{mic}) and microbial activities (basal respiration, alkaline phosphatase activity) were higher in plots treated with FYM as compared to plots treated with mineral fertiliser. At site STC, alkaline phosphatase activity was higher in plots treated with chicken manure alone than in plots treated with a combination of chicken manure and composted FYM. In all three short-term trials, principal component analysis of soil parameters mainly differentiated between BFI and AFI samples, whereas AFI samples did not differentiate depending on soil amendment or fertility input level (Fig. 6).

Overall, fertility input treatments had little effect on the suppressiveness of soils against the three pathogens included in the study (Table 6). Exceptions were (i) a significant reduction of disease caused by *H. parasitica* on *A. thaliana* grown in soils amended with composted FYM when compared to chicken manure in soil samples from site TAD and (ii) a significant weight reduction in *O. basilicum* infected with *R. solani* in soils amended with FYM compared to soils amended with mineral fertiliser in soil samples from BON.

Discussion

In the present study we have shown that soil type is a major determinant for suppressiveness against soil- as well as air-borne foliar diseases. Soil substrate composition has been identified before as a main determinant for soil microbial community structure and, in consequence, for suppressiveness to soil-borne diseases, as recently reviewed by (Garbeva et al. 2004). Soil microorganisms such as *Pseudomonas* sp. (De Meyer and Höfte 1997; Iavicoli et al. 2003; van Wees et al. 1997), *Serratia marescens* (Press et al. 1997), *Bacillus pumilus* (Ryu et al. 2003) or *Trichoderma hamatum* (de Meyer et al. 1998) can induce resistance in plants against foliar diseases if added to potting mixtures or natural soils. However, the potential of different soil types to suppress foliar diseases has not been quantified so far. In the present study, the soil types very well differentiated in the bioassay *A. thaliana – H. parasitica*, indicating that differences in susceptibility due to soil types may be relevant in agricultural production systems. Under controlled conditions, susceptibility of plants growing on different soil types differed by a factor of up to four, while most other studies on rhizobacteria-mediated induced systemic resistance report about smaller disease reductions up to a factor of two (De Meyer et al. 1999; Iavicoli et al. 2003; Pieterse et al. 1996).

We hypothesize that soil microorganisms rather than chemical or physical parameters are responsible

Table 3 General chemical parameters (pH, cation exchange capacity), C total, N total and macronutrients of soils under examination. Results of each site except DOK were subjected to an ANOVA (α=0.05) and a posthoc Tukey-B test to test for significant differences between strategies. Bold letters stand for a significant ANOVA, and different letters indicate significant differences in the Tukey-B test. Regular letters stand for a non-significant ANOVA. For abbreviations of treatments see Table 1

Site	Strategy	Level	pH	Cation exchange capacity [1]	C total [2]	N total [2]	Nmin [2]	P total [2]	P (EDTA) [2]	K total [2]	K (EDTA) [2]	Ca [2]	Mg [2]	S [2]
DOK	BIODYN	0.7 LSU	5.7	11.7	13.7	1.6	1.7	25	7	111	42	2103	104	13.2
	BIOORG		5.4	10.2	12.2	1.5	2.1	30	8	114	45	1801	101	13.9
	CONFYM		5.7	10.1	14.2	1.4	2.5	37	14	121	46	1784	103	14.2
	BIODYN	1.4 LSU	6.0	13.1	16.6	1.8	2.9	34	13	156	65	2326	127	15.5
	BIOORG		6.0	10.9	14.3	1.6	1.5	37	15	172	74	1867	122	12.2
	CONFYM		5.9	10.6	15.4	1.5	2.2	57	28	183	76	1812	128	14.8
	CONMIN		5.4	10.7	11.7	1.5	2.3	56	27	178	64	1810	138	13.4
	NOFERT	0 LSU	5.0	10.1	14.2	1.4	1.6	24	6	79	29	1835	83	13.5
BON	BFI		**6.7 a**	7.2	11.1	0.7	**2.2 a**	70	43	224	**125 a**	1162	92	9.6
	FYM	85 kg ha^{-1}	**6.4 bc**	7.0	13.9	1.0	**2.5 ab**	69	37	179	**91 ab**	1166	88	9.5
	CompFYM		**6.4 bc**	6.9	13.6	1.0	**2.1 a**	76	39	156	**89 ab**	1139	90	9.8
	MIN		**6.4 bc**	6.9	13.3	1.0	**3.4 ab**	73	38	155	**69 b**	1148	88	8.8
	FYM	170 kg ha^{-1}	**6.5 b**	6.8	13.7	1.0	**2.5 ab**	64	41	148	**121 a**	1137	87	8.2
	CompFYM		**6.5 bc**	7.0	14.2	1.0	**3.5 ab**	73	42	165	**114 a**	1156	93	9.1
	MIN		**6.4 c**	6.8	12.4	1.0	**4.0 b**	72	36	150	**66 b**	1131	89	9.1
STC	BFI		7.0	8.7	17.0	1.1		219	**109 a**	163	92	1318	205	**13.0 a**
	CompFYM	170 kg ha^{-1}	6.9	8.8	18.2	1.1		233	**123 b**	188	99	1296	219	**15.4 b**
	ChickMan		7.0	8.9	21.1	1.1		242	**118 ab**	201	107	1317	220	**14.2 ab**
	ChickMan + CompFYM		6.8	10.1	15.0	1.2		208	**115 ab**	194	103	1518	231	**14.2 ab**
TAD	BFI		7.2	19.4	29.9	1.8		76	70	444	190	2792	518	14.2
	CompFYM	170 kg ha^{-1}	7.3	19.8	33.7	1.9		114	104	621	277	2747	541	16.2
	ChickMan		7.3	19.1	33.0	1.8		90	84	483	214	2656	553	16.8
	ChickMan + CompFYM		7.3	19.6	33.4	1.9		114	107	488	230	2781	530	16.1

[1] cmol kg^{-1} ; [2] mg kg^{-1}

Table 4 Micronutrient content of soils under examination (mg kg^{-1}). Results of each site except THE (no replicates) were subjected to an ANOVA (α=0.05) and a posthoc Tukey-B test to test for significant differences between strategies. Bold letters stand for a significant ANOVA, and different letters indicate significant differences in the Tukey-B test. Regular letters stand for a non-significant ANOVA. For abbreviations of treatments see Table 1

Site	Strategy	Level	Na	Cu	Zn	Mn	Fe	B	Al	Cd	Ni	Pb
DOK	BIODYN	0.7 LSU	14.4	5.4	4.0	154	199	0.3	798	0.1	2.1	5.1
	BIOORG		12.5	6.0	4.3	159	230	0.1	835	0.1	2.3	5.3
	CONFYM		10.1	6.1	4.4	157	232	0.2	819	0.1	2.2	5.2
	BIODYN	1.4 LSU	15.4	5.6	5.2	157	199	0.5	771	0.1	2.1	5.5
	BIOORG		21.1	5.7	4.3	135	187	0.2	701	0.1	1.9	4.9
	CONFYM		14.6	5.7	5.0	157	239	0.3	783	0.1	2.2	5.1
	CONMIN		12.5	5.8	3.6	136	217	0.2	827	0.1	2.2	4.8
	NOFERT	0 LSU	18.1	5.2	3.4	166	232	0.1	892	0.1	2.5	5.2
BON	BFI		6.0	5.5	18.6	280	293	0.1	460	0.3	2.1	18.2
	FYM	85 kg ha^{-1}	10.0	5.4	17.2	280	294	0.1	456	0.3	2.0	18.3
	CompFYM		7.6	5.9	19.1	295	313	0.1	476	0.3	2.1	17.1
	MIN		9.7	5.8	18.5	287	294	0.1	455	0.3	2.0	18.2
	FYM	170 kg ha^{-1}	10.4	5.3	16.8	273	289	0.1	454	0.3	2.0	17.8
	CompFYM		10.7	5.7	18.2	282	300	0.1	473	0.3	2.1	17.4
	MIN		9.2	5.5	18.0	284	299	0.1	462	0.3	2.0	17.6
STC	BFI		**4.9 a**	4.8	5.6	22	**430 a**	0.4	573	0.2	0.7	19.9
	CompFYM	170 kg ha^{-1}	**12.4 ab**	4.3	5.2	19	**432 a**	0.4	602	0.2	0.7	20.3
	ChickMan		**11.2 ab**	4.7	6.3	22	**387 b**	0.4	573	0.2	0.6	20.5
	ChickMan + CompFYM		**19.5 b**	4.5	6.7	20	**384 b**	0.5	528	0.2	0.6	20.1
TAD	BFI		15.0	23.4	16.2	283	225	2.1	573	**0.2 a**	**0.7 a**	**19.9 a**
	CompFYM	170 kg ha^{-1}	21.8	24.5	16.2	273	235	2.1	555	**0.3 b**	**1.4 b**	**14.8 b**
	ChickMan		15.4	22.8	17.3	288	224	2.1	592	**0.3 b**	**1.5 c**	**14.4 b**
	ChickMan + CompFYM		19.0	23.8	17.6	266	230	2.1	556	**0.3 b**	**1.4 b**	**14.3 b**

Table 5 Microbial biomass and parameters of microbial activity of soils under examination. Results of each site except THE were subjected to an ANOVA (α=0.05) and a posthoc Tukey-B test to test for significant differences between strategies. Bold letters stand for a significant ANOVA, and different letters indicate significant differences in the Tukey-B test. Regular letters stand for a non-significant ANOVA. For abbreviations of treatments see Table 1

Site	Strategy	Level	C_{mic} [1]	N_{mic} [1]	C_{mic}/N_{mic}	C_{mic}/Corg	Basal respiration [2]	qCO2 [3]	Alkaline phosphatase activity [4]	Protease activity [5]	Dehydrogenase activity [6]	Fluorecein diacetate hydrolysis [7]
DOK	BIODYN	0.7 LSU	353	52	6.7	25.7	0.67	0.52	0.33	137	10.2	1.7
	BIOORG		326	46	7.0	26.7	0.70	0.58	0.25	135	9.0	1.5
	CONFYM		305	44	7.0	21.5	0.62	0.55	0.22	137	9.2	1.7
	BIODYN	1.4 LSU	432	68	6.4	26.0	0.75	0.47	0.42	182	12.7	1.9
	BIOORG		356	53	6.8	25.0	0.70	0.53	0.30	178	12.0	1.7
	CONFYM		311	43	7.2	20.2	0.66	0.58	0.26	138	10.0	1.9
	CONMIN		272	37	7.4	23.3	0.56	0.56	0.23	124	7.5	1.5
	NOFERT	0 LSU	252	31	8.1	17.8	0.50	0.54	0.19	80	6.4	1.5
BON	BFI		**234 a**	**49 a**	4.8	21.8	**0.67 a**	0.78	**0.25 a**	**144 a**	**7.7 a**	0.9
	FYM	85 kg ha^{-1}	**203 abc**	**42 bc**	4.8	16.9	**0.54 b**	0.72	**0.27 a**	**113 ab**	**5.5 b**	0.8
	CompFYM		**182 bc**	**39 bc**	4.6	15.9	**0.50 b**	0.75	**0.28 ab**	**109 b**	**6.2 b**	0.8
	MIN		**172 c**	**37 c**	4.6	14.5	**0.48 b**	0.77	**0.26 a**	**102 b**	**6.0 b**	0.8
	FYM	170 kg ha^{-1}	**218 ab**	**44 ab**	4.9	16.2	**0.59 ab**	0.73	**0.31 b**	**129 ab**	**5.8 b**	0.9
	CompFYM		**180 bc**	**40 bc**	4.5	13.9	**0.51 b**	0.79	**0.28 ab**	**120 ab**	**6.1 b**	0.8
	MIN		**162 c**	**36 c**	4.4	13.9	**0.50 b**	0.88	**0.26 a**	**120 ab**	**6.2 b**	0.8
STC	BFI		145	27	5.3	8.5	**0.51 a**	**0.99 a**	**0.31 a**	**70 a**	2.7	**0.5 a**
	CompFYM	170 kg ha^{-1}	117	24	4.9	6.8	**0.77 b**	**1.81 b**	**0.43 ab**	**112 b**	3.0	**0.2 b**
	ChickMan		146	26	5.6	7.1	**0.85 b**	**1.60 b**	**0.50 b**	**114 b**	3.6	**0.2 b**
	ChickMan + CompFYM		100	19	5.3	6.8	**0.68 ab**	**1.84 b**	**0.30 a**	**101 b**	2.4	**0.2 b**
TAD	BFI		**354 a**	68	**5.2 a**	11.8	**1.42 a**	1.10	0.60	90	10.3	0.7
	CompFYM	170 kg ha^{-1}	**391 ab**	70	**5.6 b**	11.7	**1.57 ab**	1.10	0.77	62	10.0	0.8
	ChickMan		**426 b**	75	**5.7 b**	13.1	**1.78 b**	1.14	0.74	62	11.2	0.7
	ChickMan + CompFYM		**396 ab**	71	**5.6 b**	12.0	**1.62 ab**	1.12	0.74	66	10.0	0.7

[1] mg kg^{-1} ; [2] mg CO_2 g^{-1} soil h^{-1} ; [3] mg CO_2–C g^{-1} (C_{mic}) h^{-1} ; [4] mg Nitrophenol g^{-1} h^{-1} ; [5] µg Tyrosin eq. g^{-1} soil 2 h^{-1} ; [6] mg TPF g^{-1} soil h^{-1} ; [7] µg FDAhy g^{-1} soil(dry weight) min^{-1}

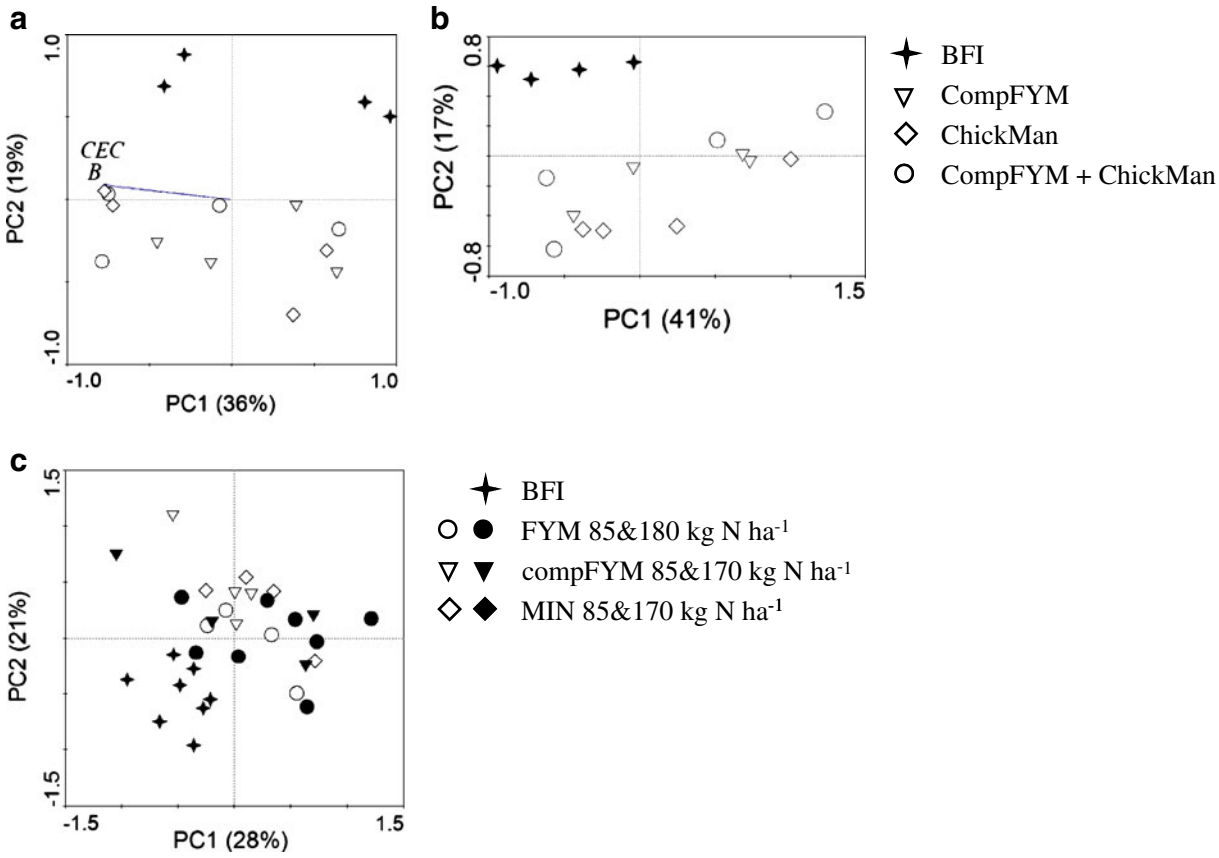

Fig. 6 Ordination of the first two ordination axes as determined by principal component analysis (PCA) of soil chemical and biological parameters of the three short-term fertility input trials at sites (**a**) Bonn (BON), (**b**) Stocksbridge (STC) or (**c**) Tadcaster (TAD). For abbreviations of the treatments see Table 1. The percentage of explained variance is displayed in parentheses along the first two ordination axes. Arrows show parameters contributing most to the first principal components (species fit >90%). B boron, CEC cation exchange capacity

for the observed differences, since suppressiveness against soil- as well as air-borne diseases could be significantly reduced by sterilisation of the soils by γ-irradiation (Thuerig et al. 2009). Depending on soil composition and origin, different microorganisms and/or mechanisms are likely to be involved in disease suppressiveness against pathogenic species, since none of the soil types under study was suppressive against all four diseases. The causal organisms and the involved mechanisms such as competition, antibiosis, hyperparasitism and the induction of plant disease resistance (Haas and Défago 2005) have not yet been identified and the relative importance of the involved mechanisms may vary, depending on the host-pathogen system under study (Janvier et al. 2007). However, the emphasis of this study was placed on the quantification of suppressiveness against a range of pathogens and on the identification of effects that may have relevance in agricultural systems.

In the present study, we have shown that site-specific suppressiveness can be modulated by long-term soil management as well as, to a limited extent, by short-term fertility inputs. It has been demonstrated before that suppressiveness of natural soils to soil-borne diseases can be improved by the application of organic soil amendments such as manure and composts (Fuchs 2002; Litterick et al. 2004), either by promoting beneficial microorganisms native to the soils and/or by introducing new beneficial microorganisms (Chu et al. 2007; Inbar et al. 2005; Innerebner et al. 2006; Pérez-Piqueres et al. 2006; Serra-Wittling et al. 1996; Van Elsas et al. 2002). The effect of such amendments on the resistance of host plants to air-

Table 6 Overview of the effects of short-term fertility management on three plant-pathogen systems. Results of each site were subjected to an ANOVA (α=0.05) and a posthoc Tukey-B test to test for significant differences between strategies. Bold letters stand for a significant ANOVA, and different letters indicate significant differences in the Tukey-B test. Regular letters stand for a non-significant ANOVA. For abbreviations of treatments see Table 1

Site	Strategy	Level	*O. basilicum* - *R. solani*		*L. esculentum*-*P. infestans*[2]	*A. thaliana* – *H. parasitica* [3]
			Weight without *R. solani* (g)	Weight reduction[1]		
BON	FYM	85 kg ha^{-1}	**2.06 bc**	**−42% ab**	1.00 a	1.03 a
	CompFYM		**1.71 ab**	**−44% ab**	1.00 a	1.06 a
	MIN		**1.43 a**	**−31% a**	0.94 a	0.92 a
	FYM	170 kg ha^{-1}	**2.39 c**	**−46% b**	1.01 a	1.02 a
	CompFYM		**2.15 c**	**−39% ab**	1.07 a	0.96 a
	MIN		**1.74 ab**	**−30% a**	0.97 a	1.01 a
STC	CompFYM	170 kg ha^{-1}	1.43 a	−21% a	0.99 a	0.98 a
	ChickMan		1.56 a	−15% a	0.99 a	1.03 a
	ChickMan + CompFYM		1.54 a	−25% a	1.02 a	1.00 a
TAD	CompFYM	170 kg ha^{-1}	3.33 a	−35% a	1.03 a	**0.81 b**
	ChickMan		3.85 a	−42% a	0.93 a	**1.13 a**
	ChickMan + CompFYM		3.85 a	−38% a	1.04 a	**1.08 ab**

[1] reduction in shoot fresh weight of *O. basilicum* by *R. solani* compared to unchallenged soils

[2] relative lesion diameter calculated as lesion diameter * mean lesion diameter experiment^{-1}

[3] relative leaf area covered with sporangiaphores calculated as severity * mean severity experiment^{-1}

borne diseases has not been intensively studied so far. For instance, one study has shown that composted paper mill residues amended to field soils can reduce air-borne disease caused by *Pseudomonas syringae* pv. *tomato* in *A. thaliana* and tomato (Vallad et al. 2003). In the present study, in the bioassay *A. thaliana* – *H. parasitica*, suppressiveness was positively correlated to soil microbial biomass (data not shown) if grown on soils from the DOK-long-term trial where long-term soil management strategies have affected soil physical, chemical and biological characteristics (Mäder et al. 2002). We thus speculate that the long-term application of organic amendments might have promoted soil microorganisms inducing systemic resistance in plants. Further studies should aim at verifying this hypothesis by analysing expression patterns of defense-related genes primed in ISR and to identify involved microorganisms.

The short-term effect of fertility inputs on soil parameters as well as on suppressivenes was more limited than the effects of long-term management. Differences were mainly found between soil samples taken before and after fertility input amendments and between soils fertilised exclusively with either organic or mineral fertilisers. This observation is in accordance with results from the DOK-trial, where the application of FYM as opposed to mineral fertiliser has been identified as a key factor for differentiation of various soil parameters:(Widmer et al. 2001) The application of organic amendments is thought to result in a general enrichment in organic substrates, therefore promoting growth of microbial communities. Yet, such changes in stable systems are supposed to occur over prolonged time-periods, and only after repetitive application of organic matter based soil amendments.

In conclusion, we have shown that soils can not only affect the development of soil-borne, but also the resistance of plants to air-borne diseases. Site-specific properties such as soil types had a larger effect than cultivation-specific effects within the same site. Nevertheless, short-term, but in particular long-term management strategies have been shown to have the potential to influence suppressiveness of soils.

Acknowledgements The authors gratefully acknowledge funding from the European Community financial participation under the Sixth Framework Programme for Research, Technological Development and Demonstration Activities, for the Integrated Project QUALITYLOWINPUTFOOD, FP6-FOOD-

CT-2003-506358. We are grateful to Sabine Rattler, Bonn, and many students who helped us in soil sampling and preparation.

References

Alef, K., & Nannipieri, P. (1995). *Methods in applied soil microbiology and biochemistry*. London: Academic Press Limited.

Berner, A., Gloor, S., Fuchs, J. G., Tamm, L., & Mäder, P. (2002). *Healthy soils - healthy plants*. Paper presented at the 14th IFOAM Organic World Congress, Victoria, Canada.

Blume, H.-P., Deller, B., Leschber, R., Paetz, A., Schmidt, S., & Wilke, B.-M. (2000). *Handbuch der Bodenuntersuchung*. Berlin: Beuth.

Bossio, D. A., Scow, K. M., Gunpala, N., & Graham, K. J. (1998). Determination of soil microbial communities: effect of agricultural management, season, and soil type on phospholipid fatty acid profiles. *Microbial Ecology, 36*, 1–12.

Brookes, P. C., Landman, A., Pruden, G., & Jenkinson, D. S. (1985). Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology & Biochemistry, 17*, 837–842.

Chu, H., Lin, X., Fujii, T., Morimoto, S., Yagi, K., Hu, J., et al. (2007). Soil microbial biomass, dehydrogenase activity, bacterial community structure in response to long-term fertilizer management. *Soil Biology & Biochemistry, 39*, 2971–2976.

De Meyer, G., & Höfte, M. (1997). Salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 induces resistance to leaf infection by *Botrytis cinerea* on bean. *Phytopathology, 87*, 588–593.

De Meyer, G., Bigirimana, J., Elad, Y., & Höfte, M. (1998). Induced systemic resistance in *Trichoderma harzianum* T39 biocontrol of *Botrytis cinerea*. *European Journal of Plant Pathology, 104*, 279–286.

De Meyer, G., Capieau, K., Audenaert, K., Buchala, A., Métraux, J.-P., & Höfte, M. (1999). Nanogram amounts of salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 activate the systemic acquired resistance pathway in bean. *Molecular Plant Microbe Interactions, 12*, 450–458.

Doran, J. W., Sarrantonio, M., & Lieberg, M. A. (1996). Soil health and sustainability. *Advances in Agronomy, 56*, 1–54.

Fuchs, J. G. (2002). Practical use of quality compost for plant health and vitality improvement. In H. Insam, N. Riddech, & S. Klammer (Eds.), *Microbiology of composting* (pp. 435–444). Heidelberg: Springer Verlag.

Garbeva, P., Van Veen, J. A., & Van Elsas, J. D. (2004). Microbial diversity in soil: Selection of microbial populations by plant and soil type and implications for disease suppressiveness. *Annual Review of Phytopathology, 42*, 243–270.

Govaerts, B., Mezzalama, M., Unno, Y., Sayre, D. D., Luna-Guido, M., Vanherck, K., et al. (2007). Influence of tillage, residue management, and crop rotation on soil microbial biomass and catabolic diversity. *Applied Soil Ecology, 37*, 18–30.

Haas, D., & Défago, G. (2005). Biological control of soil-borne pathogens by fluorescent pseudomonads. *Nature Reviews Microbiology, 3*, 307–319.

Hoitink, H. A. J., Van Doren, D. M. J., & Schmitthenner, A. F. (1977). Suppression of *Phytophthora cinnamomi* in a composted hardwood bark potting medium. *Phytopathology, 67*, 561–565.

Iavicoli, A., Boutet, E., Buchala, A., & Métraux, J. P. (2003). Induced systemic resistance in *Arabidopsis thaliana* in response to root inoculation with *Pseudomonas fluorescens* CHA0. *Molecular Plant Microbe Interactions, 10*, 851–858.

Inbar, E., Green, S. J., Hadar, Y., & Minz, D. (2005). Competing factors of compost concentration and proximity to root affect the distribution of streptomycetes. *Microbial Ecology, 50*, 73–81.

Innerebner, G., Knapp, B., Vasara, T., Romantschuk, M., & Insam, H. (2006). Traceability of ammonia-oxidizing bacteria in compost-treated soils. *Soil Biology & Biochemistry, 38*, 1092–1100.

Jäggi, W. (1976). Die Bestimmung der CO_2-Bildung als Mass der bodenbiologischen Aktivität. *Schweizerische Landwirtschaftliche Forschung, 15*, 371–380.

Janvier, C., Villeneuve, F., Alabouvette, C., Edel-Hermann, V., Mateille, T., & Steinberg, C. (2007). Soil health through soil disease suppression: which strategy from descriptors to indicators? *Soil Biology and Biochemistry, 39*, 1–23.

Kandeler, E. (1993). Bestimmung der Aggregatstabilität. In F. Schinner, R. Öhlinger, E. Kandeler, & R. Margesin (Eds.), *Bodenbiologische Arbeitsmethoden* (pp. 351–355). Berlin: Springer.

Kloepper, J. E., Rodriguez-Ubana, R., Zehnder, G. W., Murphy, J. F., Sikora, E., & Fernandez, C. (1999). Plant root-bacterial interactions in biological control of soilborne diseases and potential extension to systemic and foliar diseases. *Australasian Plant Pathology, 28*, 21–26.

Knudsen, I. M. B., Larsen, K. M., Jensen, D. F., & Hockenhull, J. (2002). Potential suppressiveness of different field soils to *Pythium* damping-off of sugar beat. *Applied Soil Ecology, 21*, 119–129.

Litterick, A. M., Harrier, L., Wallace, C., Watson, C. A., & Wood, M. (2004). The role of uncomposted materials, composts, manures, and compost extracts in reducing pest and disease incidence and severity in sustainable temperate agricultural and horticultural crop production - A review. *Critical Reviews in Plant Sciences, 23*, 453–479.

Mäder, P., Fließbach, A., Dubois, D., Gunst, L., Fried, P., & Niggli, U. (2002). Soil fertility and biodiversity in organic farming. *Science, 296*, 1694–1697.

Mäder, P., Fließbach, A., Dubois, D., Gunst, L., Jossi, W., Widmer, F., et al. (2006). The DOK experiment (Switzerland). In J. Raupp, C. Pekrun, M. Oltmanns, & U. Köpke (Eds.), *Long-term field experiments in organic farming* (pp. 41–58). Bonn: Koester.

Mehlich, A. (1984). Mehlich-3 soil test extractant: a modification of Mehlich-2 extractant. *Communications in Soil Science and Plant Analysis, 15*, 1409–1416.

Menzies, J. G. (1959). Occurrence and transfer of a biological factor in soil that suppresses potato scab. *Phytopathology, 49*, 648–652.

Pérez-Piqueres, A., Edel-Hermann, V., Alabouvette, C., & Steinberg, C. (2006). Response of soil microbial communities to compost amendments. *Soil Biology & Biochemistry, 38*, 460–470.

Pieterse, C. M. J., Van Wees, S. C. M., Hoffland, E., Van Pelt, J. A., & Van Loon, L. C. (1996). Systemic resistance in Arabidopsis induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. *Plant Cell, 8*, 1225–1237.

Press, C. M., Wilson, M., Tuzun, S., & Kloepper, J. W. (1997). Salicylic acid produced by *Serratia marcescens* 90–166 is not the primary determinant of induced systemic resistance in cucumber or tobacco. *Molecular Plant-Microbe Interactions, 10*, 761–768.

Rotenberg, D., Joshi, R., Benitez, M.-S., Chapin, L. G., Camp, A., Zumpetta, C., et al. (2007). Farm management effects on rhizosphere colonization by native populations of 2, 4-diacetylphloroglucinol-producing Pseudomonas spp. and their contributions to crop health. *Phytopathology, 97*, 756–766.

Ryu, C.-M., Hu, C.-H., Reddy, M. S., & Kloepper, J. E. (2003). Different signaling pathways of induced resistance by rhizobacteria in *Arabidopsis thaliana* against two pathovars of *Pseudomonas syringae*. *New Phytologist, 160*, 413–420.

Serra-Wittling, C., Houot, S., & Alabouvette, C. (1996). Increased soil suppressiveness to *Fusarium* wilt of flax after addition of municipal solid waste compost. *Soil Biology & Biochemistry, 28*, 1207–1214.

Shipton, P. J., Cook, R. J., & Sitton, J. W. (1973). Occurrence and transfer of a biological factor in soil that suppresses take-all of wheat in Eastern Washington. *Phytopathology, 63*, 511–517.

Stutz, E. W., Défago, G., & Kern, H. (1986). Naturally occurring fluorescent *Pseudomonads* involved in suppression of black root rot of tobacco. *Phytopathology, 76*, 181–185.

Tamm, L. (2001). Organic agriculture: development and state of the art. *Journal of Environmental Monitoring, 3*, 92–96.

Theodore, M., & Toribio, J. A. (1995). Suppression of *Pythium aphanidermatum* in composts prepared from sugarcane factory residues. *Plant and Soil, 177*, 219–223.

Thuerig, B., Fliessbach, A., Berger, N., Fuchs, J., Kraus, N., Mahlberg, N., et al. (2009). Re-establishment of suppressiveness to soil- and air-borne diseases by re-inoculation of soil microbial communities. *Soil Biology & Biochemistry*,

Vallad, G. E., Cooperband, L., & Goodman, R. M. (2003). Plant foliar disease suppression mediated by composted forms of paper mill residuals exhibits molecular features of induced resistance. *Physiological and Molecular Plant Pathology, 63*, 65–77.

Vance, E. D., Brookes, P. C., & Jenkinson, D. S. (1987). An extraction method for measuring soil microbial biomass C. *Soil Biology & Biochemistry, 19*, 703–707.

Van Elsas, J. D., Garbeva, P., & Salles, J. (2002). Effects of agronomical measures on the microbial diversity of soils as related to the suppression of soil-borne plant pathogens. *Biodegradation, 13*, 29–40.

Van Loon, L. C., & Bakker, A. H. M. (2005). Induced systemic resistance as a mechanism of disease suppression by rhizobacteria. In Z. A. Siddiqui (Ed.), *PGPR: Biocontrol and biofertilization* (pp. 39–66). Dordrecht: Springer.

Van Loon, L. C., Bakker, P. A. H. M., & Pieterse, C. M. J. (1998). Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology, 36*, 453–483.

Van Wees, S. C. M., Pieterse, C. M. J., Trijssenaar, A., Van'T Westende, Y. A. M., Hartog, F., & Van Loon, L. C. (1997). Differential induction of systemic resistance in *Arabidopsis* by biocontrol bacteria. *Molecular Plant-Microbe Interactions, 10*, 716–724.

Widmer, F., Fliessbach, A., Laczko, E., Schulze-Aurich, J., & Zeyer, J. (2001). Assessing soil biological characteristics: a comparison of bulk soil community DNA-, PLFA-, and Biolog™-analyses. *Soil Biology & Biochemistry, 33*, 1029–1036.

Wiseman, B. M., Neate, S. M., Keller, K. O., & Smith, S. E. (1996). Suppression of *Rhizoctonia solani* anastomosis group 8 in Australia and its biological nature. *Soil Biology & Biochemistry, 28*, 727–732.