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Effects on growth of wheat plants of isolates of *Gaeumannomyces/Phialophora*-complex fungi in different conditions of soil moisture, temperature, and photoperiod

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Abstract

The effects on spring wheat (*Triticum aestivum* L., cv. Mario) of nine isolates of the *Gaeumannomyces/Phialophora* complex, ranging from non-pathogenic to pathogenic, were studied under different conditions of soil moisture, soil temperature, and photoperiod in growth chambers which simulated different autumn weather conditions. The experimental conditions were based on data (e.g. temperature) from representative sites (loamy sand, Muencheberg, Northeast Germany) collected in the last three decades. The results of seedling inoculation tests for four non-pathogenic isolates were partly in agreement with results from field trials done over 4 years. One non-pathogenic *G. graminis* var. *tritici* isolate (G 33) increased consistently dry weight of shoots in the simulation, and grain yield in field experiments. For non-pathogenic isolates, warm temperatures with moderate soil moisture most often stimulated plant growth, with less effect in cold dry soil conditions. The decrease in seedling growth caused by pathogenic isolates was influenced only slightly by temperature changes, but was often enhanced by increased soil moisture.

Introduction

In previous work on the biological control of take-all caused by *Gaeumannomyces graminis* (Sacc.) Arx & Oivier var. *tritici* Walker, grain yield was increased by the inoculation of wheat with non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on loamy sand sites in East Brandenburg, Northeast Germany (Augustin, 1989, 1990). A decrease in take-all disease and increased host growth occurred with weakly or non-pathogenic *G. graminis* var. *graminis* isolates or two isolates of the closely related *Phialophora graminicola* and *Phialophora* sp. (lobed hyphopodia) (Walker, 1980). However, the practical value of these microbial antagonists was limited by inconsistent performances. Genetic and physiological factors as well as the enormous ability of microorganisms to adapt to changes in their natural environment probably accounted for this variability.

Several studies (Cook and Christen, 1976; Cassel and Hering, 1982; Cotterill and Sivasithamparam, 1987, 1989; Sivasithamparam, 1993) have demonstrated that environmental conditions significantly influence the rates of infection of *G. graminis*. Therefore, in order to estimate the effects of non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on wheat plants, environmental conditions have to be taken into consideration. The temporal variability of soil moisture and soil temperature seems to be of special importance (Wong, 1983; Lucas and Nignon, 1987). To determine the effects of these isolates on plant growth, most of the tests have been carried out under constant and simplified environmental conditions in growth chamber experiments.

However, to forecast the effects of these non-pathogenic fungal isolates more accurately, variable environmental conditions should be included in more realistic experiments; experiments on isolates of the *Gaeumannomyces/Phialophora* complex were therefore done in growth chambers under different conditions of soil moisture, temperature, and day-length. The conditions simulated major features of autumn weather and the results were compared with those from long-term field experiments in which four non-pathogenic isolates were tested. The study focused on the early stages of the development of wheat in autumn, because the fungal infections by pathogenic and colonization by non-pathogenic isolates occur mostly at the seedling stage (Augustin, 1989).

Materials and methods

Plant cultivation and experimental conditions

The conditions for growing spring wheat and inoculations with fungal isolates in growth chambers have been described previously (Augustin, 1989, 1990). Test tubes containing 90 g quartz sand with 7.5 ml standard nutrient solution (10% 'Wopil' fertilizer) were sterilized (121 °C, 1.2 bar) for 1 h. Seed of *Triticum aestivum* L., cv. Mario, was surface sterilized (1% bromine solution, 30s), germinated and transferred into the tubes (1 seedling per tube). Fungal test isolates had been grown on straw (two parts wheat, one part oat) for 4 weeks and 2 g of this colonized straw was added to the test tubes. Control test tubes were not inoculated. Plants were harvested 6 weeks after inoculation. Each treatment consisted of ten individual plants. The tubes were randomly distributed in growth chambers. The distribution was changed daily after adjusting for soil moisture. Every experiment was repeated consecutively three times.

The influence of soil moisture on the effects of fungal isolates on plant growth (dry weight of shoots) was tested. For this, three moisture conditions were maintained: simulation of dry soil at 35%, moderate moisture at 60%, and increased moisture or wet conditions at 85% of the maximum water capacity (maximum water capacity of quartz sand is about 13% of the dry weight or 18% of the volume, respectively). In addition, these three moisture conditions were combined with six temperatures (measured in the substrate) and two light regimes (experiments 1 to 6). As previous experiments (Augustin, 1989, 1990) were carried out under moderate (60%) moisture conditions, the current results were comparable to those.

Experiment 1 included a combination of the three moisture conditions (dry, moderate, wet) with temperatures of 12 °C (day) and 5 °C (night) and a 14 h photoperiod of 35,000 lm m^{-2}. In experiment 2, the temperatures were increased to 18 °C during the day and 8 °C during the night. In experiment 3, the temperatures were alternated weekly: 18 °C (day) and 8 °C (night), and 8 °C (day) and 1 °C night. Environmental conditions in autumn on experimental field sites (albic luvisol; Muencheberg, Northeast Germany) were determined from weather data from the last three decades. Temperatures during September to November in 1989 (Figure 2a) represented a warm autumn (day average of 14.8 °C and night average of 6.6 °C). These daily temperatures were maintained in experiment 4. In addition, an average of the temperature courses of these months from the last three decades was maintained in experiment 5. The temperature conditions in 1979 were suitable for simulating daily temperatures (data not shown in detail) of a cold autumn regime (average at day 9.6 °C, night 2.9 °C) in experiment 6. Furthermore, to achieve realistic photoperiods of autumn, the photoperiods of the latter experiments (4 to 6) were progressively decreased from a 14 to 9 h day.

Field experiments

Field trials were carried out on loamy sand sites (location Muencheberg), normally using eight plots (four in 1987). Effects were studied on the grain yield of winter wheat (cv. Alcedo) of two kinds of inoculation (10 g straw inoculum per kg soil in 1987 and 1988; 35 kg mycelium granulate per 50 kg seed in 1989, 1990, and 1991) at sowing with non-pathogenic isolates of *G. graminis* var. *tritici* (G 33, G 56/57) and *Phialophora* sp. (P 7, P 13). The uninoculated control and inoculated variants were exposed to a natural take-all fungus population in the soil of field plots.

Fungal infections (colonizations) and the resulting plant dry matter production from growth chamber experiments 1 to 6 were compared with those from long-term field experiments on representative sites for selected non-pathogenic isolates (details in Augustin, 1990). In field trials, grain yield was measured; the effects of the isolates on wheat were assessed by this test (Augustin, 1989).

Selected fungal isolates and test for pathogenicity

Seven isolates of *G. graminis* (G 41, G 172, G 33, G 56, AV 3, 4.1a, 4.1b) and two isolates of *Phialophora* spp. (P 7, P 13) showing differences in their pathogenicity (or colonization) were tested (Table 1) as described previously (Augustin, 1989, 1990). At 6 weeks from inoculation in growth chambers, plant shoot dry weight and depth and length of roots were determined.

The data of all experiments were analysed by ANOVA (analysis of variance) and the means compared in Newman-Keuls tests.

Results

Effects of environmental conditions and test fungi on wheat growth

As expected, soil moisture, soil temperature and light conditions in the growth chamber experiments had very strong effects on plant development. With a few exceptions, plant dry matter was highest on wet soil conditions and lowest with dry soil (Figure 1a–f). Elevated soil temperatures and long photoperiods stimulated the plant growth (experiment 1–4, Figure 1a–d) whereas low soil temperature, in combination with shorter photoperiods, impeded plant growth (partly experiment 4, Figure 1d, especially experiment 5 and 6, Figure 1e and 1f). Despite this, each set of environmental conditions was connected to a specific response of plant growth to fungal inoculation.

In experiment 1 dry weights, compared with the uninoculated control, were greatest for pathogenic and non-pathogenic isolates, particularly G 33 (*G. graminis* var. *tritici*, non-pathogenic) and P 7 (*P. graminicola)* at moderate (60%) soil moisture (Figure 1a). In experiment 2, the plant growth-promoting effects of the non-pathogenic isolates were greatest with moderate soil moisture (Figure 1b). In experiment 3, with alternating high and low temperatures on a weekly basis, the growth-promoting effects of some of the non-pathogenic isolates disappeared, especially with moderate soil moisture. Isolates AV 3, G 56, 4.1a (*G. graminis* var. *tritici*), P 7 (*P. graminicola*), and P 13 (*Phialophora* sp. (lobed hyphopodia)) decreased plant growth (Figure 1c). In contrast, pathogenic isolates G 41 and G 172 (*G. graminis* var. *tritici*) did not decrease plant growth under dry (35%) soil moisture conditions. In experiments 4 to 6, the environmental conditions of three experiments were determined by different, but typical autumn weather records. A comparison between the three experiments revealed the following. With decreasing temperatures (decreasing from experiment 4 to 6), the effects of the inoculated fungal isolates became more distinct. Non-pathogenic isolates led to increased wheat plant growth with higher temperatures (warm autumn, experiment 4, Figure 1d) and with medium and high soil moisture. Conversely, with low temperatures (cool autumn, experiment 6, Figure 1f) this was the case only with dry soil. Damage was mainly expressed under moderate and wet soil conditions. Only the non-pathogenic isolate G 33 enhanced plant development in all tested conditions; this isolate had proven to be reliable as biological control agent against take-all in field experiments (see below).

Comparison of non-pathogenic isolates under field conditions

There were similar trends in grain yield data for non-pathogenic isolates in field trials (Table 2, Figure 2a and b) and data from the growth chambers (Figure 1d–f). In growth chamber experiments based on typical autumn conditions (Figure 1e), the non-pathogenic *G. graminis* isolate G 33 was most effective in stimulating plant growth and it also caused consistent yield increases in the field trial conditions shown in Figures 2a and b. This was the case independently of both the length of experiments and the different test parameters used in growth chambers (dry weight of shoots) and field trials (grain yield). The non-pathogenic fungal isolate G 33, which had overall positive effects in the growth chamber experiments, also caused a significant increase in yield in all years, despite considerably different autumn weather conditions (Figures 2a and b). The effects of fungal isolates were inconsistent in field experiments, agreeing with results from the growth chamber experiments. For example, in 1988, isolates P 7 (*P. graminicola*) and P 13 (*Phialophora* sp. (lobed hyphopodia)) did not increase grain yield, nor did isolate G 56/57 (*G. graminis*) in 1989 (Table 2). Experiment 4 (Figure 1d) showed a close similarity with autumn conditions of 1987 (warm and wet, Figures 2a and b) and those in experiment 6 (Figure 1f) were comparable with the real conditions in 1989 (cold and moderate soil moisture, Figures 2a and b). In these cases and after inoculations with the isolates P 7 (*P. graminicola*), P 13 (*Phialophora* sp. (lobed hyphopodia)), and G 56/57 (*G. graminis*), only weak effects on plant development were detected.

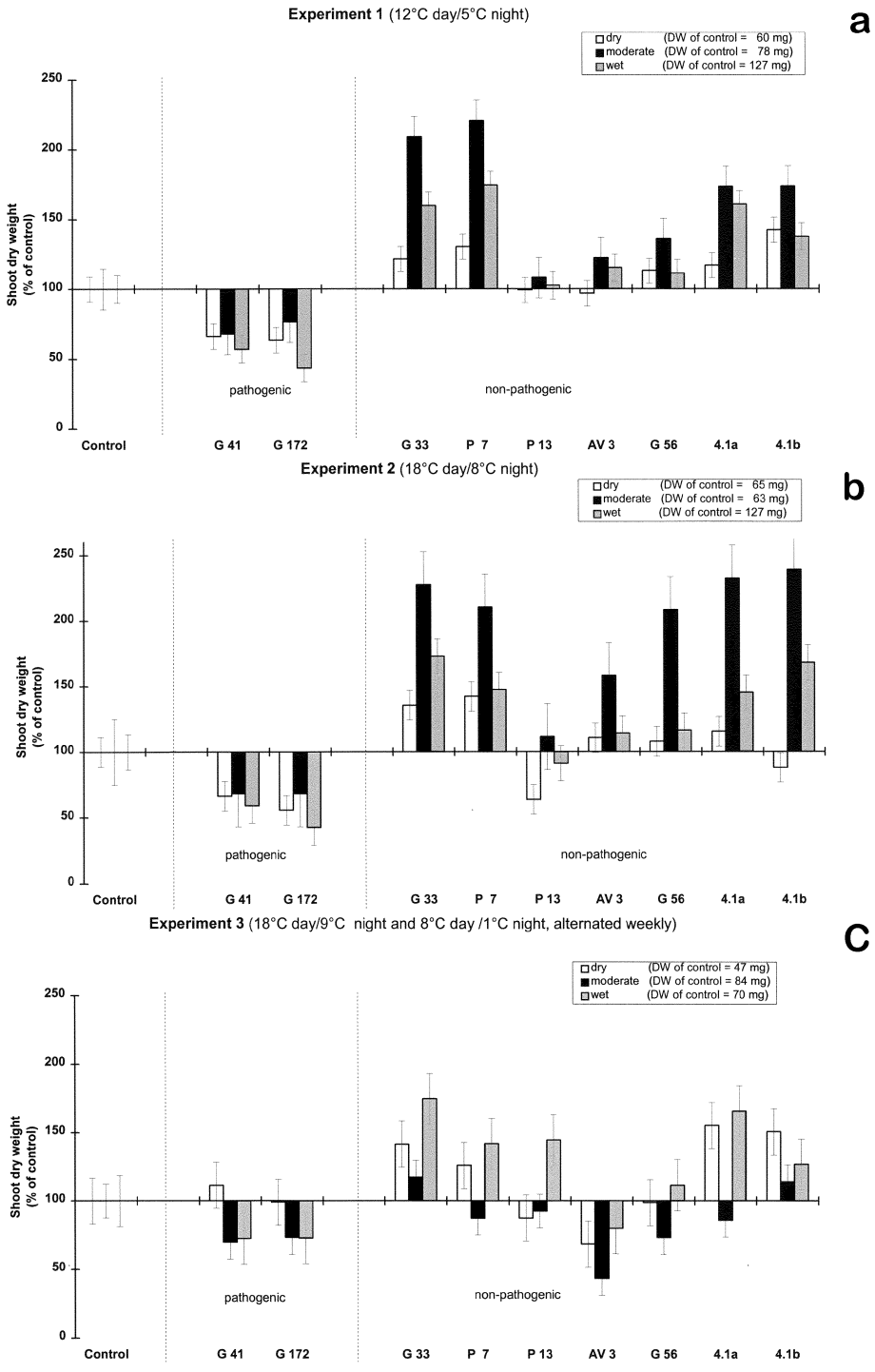

Figure 1a–c. Influence of soil moisture (dry, moderate, wet) and temperature on the effects of pathogenic and non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on the shoot dry weight of wheat (*Triticum aestivum*, cv. Mario; 6-week-old plants). Simulation of constant temperature and photoperiod conditions in growth chamber experiments 1 and 2; simulation of constant photoperiod conditions and a weekly alternated temperature regime in experiment 3. Dry weight (DW; ⊥, ⊤ = standard deviation) of shoots (inoculated plants) is given as percentage of the uninoculated control (DW in mg is given in the figure legends; n = 10; three replicates).

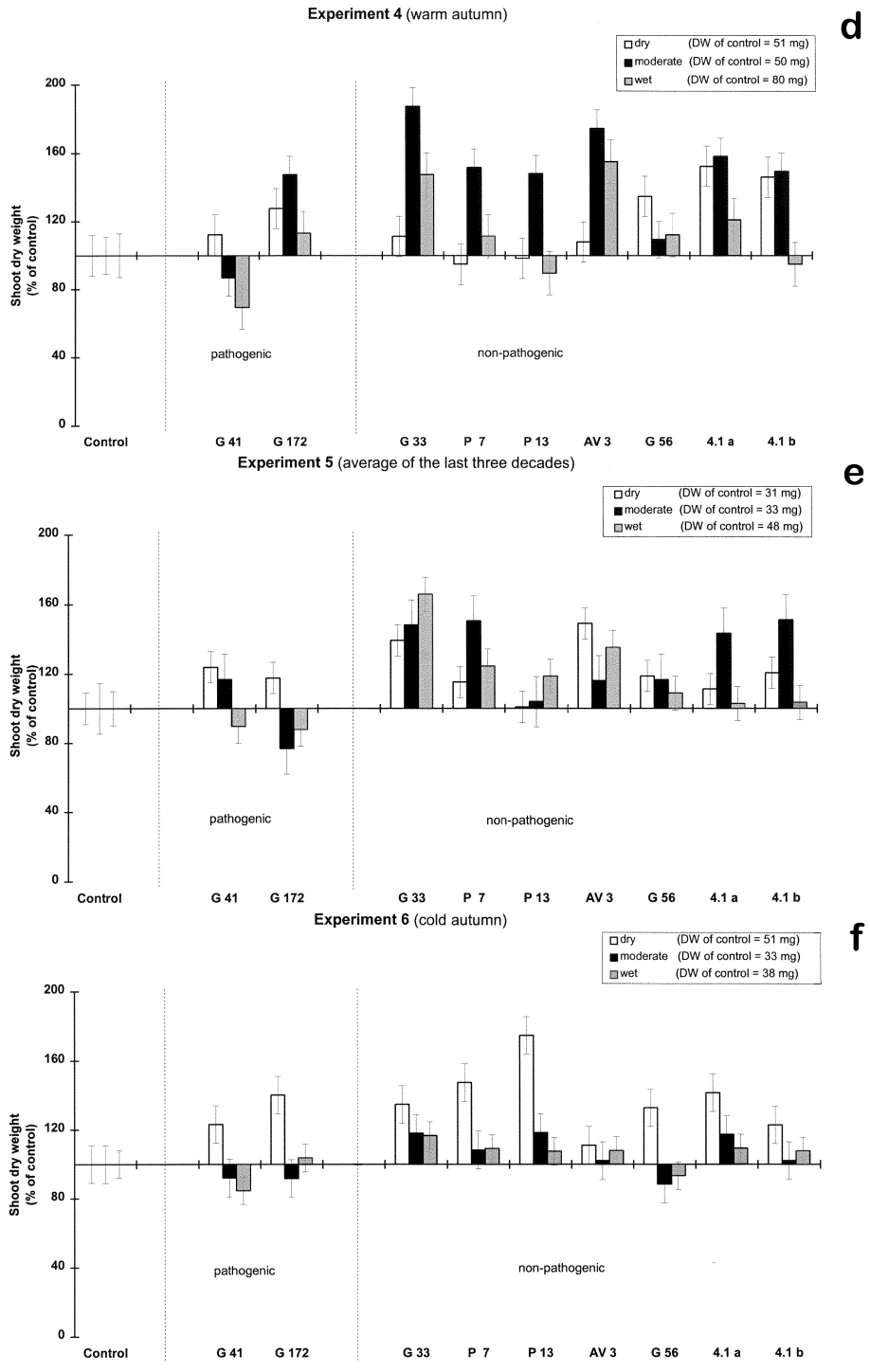

Figure 1d–f. Influence of soil moisture (dry, moderate, wet) and temperature on the effects of pathogenic and non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on the shoot dry weight of wheat (*Triticum aestivum*, cv. Mario; 6-week-old plants). Simulation of variable autumn environmental conditions and a reduced photoperiod (from 14 to 9 h) in the growth chamber experiments 4, 5, and 6. Dry weight of shoots (DW; ⊥, ⊤ = standard deviation) is given as percentage of the uninoculated control (DW in mg is given in the figure legends; n = 10; three replicates).

Table 1. *Gaeumannomyces/Phialophora* complex isolates used in the study

Isolate	Host	Geographical origin	Year of isolation	Identified as
G 41	winter barley (*Hordeum vulgare*)	Germany, Dedelow	1985	*Gaeumannomyces graminis* var. *tritici*
G 172	winter wheat (*Triticum aestivum*)	Germany, Dedelow	1987	*Gaeumannomyces graminis* var. *tritici*
G 33	winter barley (*Hordeum vulgare*)	Germany, Dedelow	1985	*Gaeumannomyces graminis* var. *tritici*
P 7	unknown	Czech Republic (fungus collection)	1986	*Phialophora graminicola*
P 13	unknown	Czech Republic (fungus collection)	1986	*Phialophora* sp. (lobed hyphopodia)
AV 3	winter wheat (*Triticum aestivum*)	Germany, Muencheberg	1987	*Gaeumannomyces graminis* var. *tritici*
G 56	winter rye (*Secale cereale*)	Germany, Muencheberg	1985	*Gaeumannomyces graminis* var. *tritici*
4.1a	grass (fallow)	Germany, Muencheberg	1987	*Gaeumannomyces graminis* var. *tritici*
4.1b	grass (fallow)	Germany, Muencheberg	1987	*Gaeumannomyces graminis* var. *tritici*
G 57	winter rye (*Secale cereale*)	Germany, Muencheberg	1985	*Gaeumannomyces graminis* var. *tritici*

Table 2. Effects of two methods of inoculation at sowing with isolates of *G. graminis* var. *tritici* (G) and *Phialophora* sp. (P) on the grain yield of winter wheat (cv. Alcedo)

Year	1987[1]	1988[1]	1989[2]	1990[2]	1991[2]	Mean
Control in %	100	100	100	100	100	100
Grain yield t ha^{-1}	5.98	7.05	6.0	6.43	4.17	5.93
+ G 33[3]	–	107.5*	116.7*	113.3*	119.4*	114.2
+ G 56/ G57	–	107.5*	110.6	–	–	109.3
+ P 7	–	103.4	120.1*	109.5*	112.9*	111.5
+ P 13	109.0*	104.4	118.4*	117.7*	114.5*	112.8
LSD ($P = 0.05$)	8.5	7.5	13.0	8.8	12.3	

* Significant differences from the control.
[1] 10 g straw inoculum per kg soil.
[2] 35 kg mycelium granulate per 50 kg seed.
[3] See Table 1 for details. Field trials on loamy sand sites (location Muencheberg), mean of eight plots (four in 1987) given as percentage of control. The uninoculated control and inoculated variants were exposed to a natural take-all fungus population in the soil of field plots.

Discussion

A major prerequisite of any biological control method is consistency of performance under different environmental conditions in order to be accepted into agricultural practice. Improved biological control of take-all could be achieved by the development of simplified methods (without long-term field experiments) which

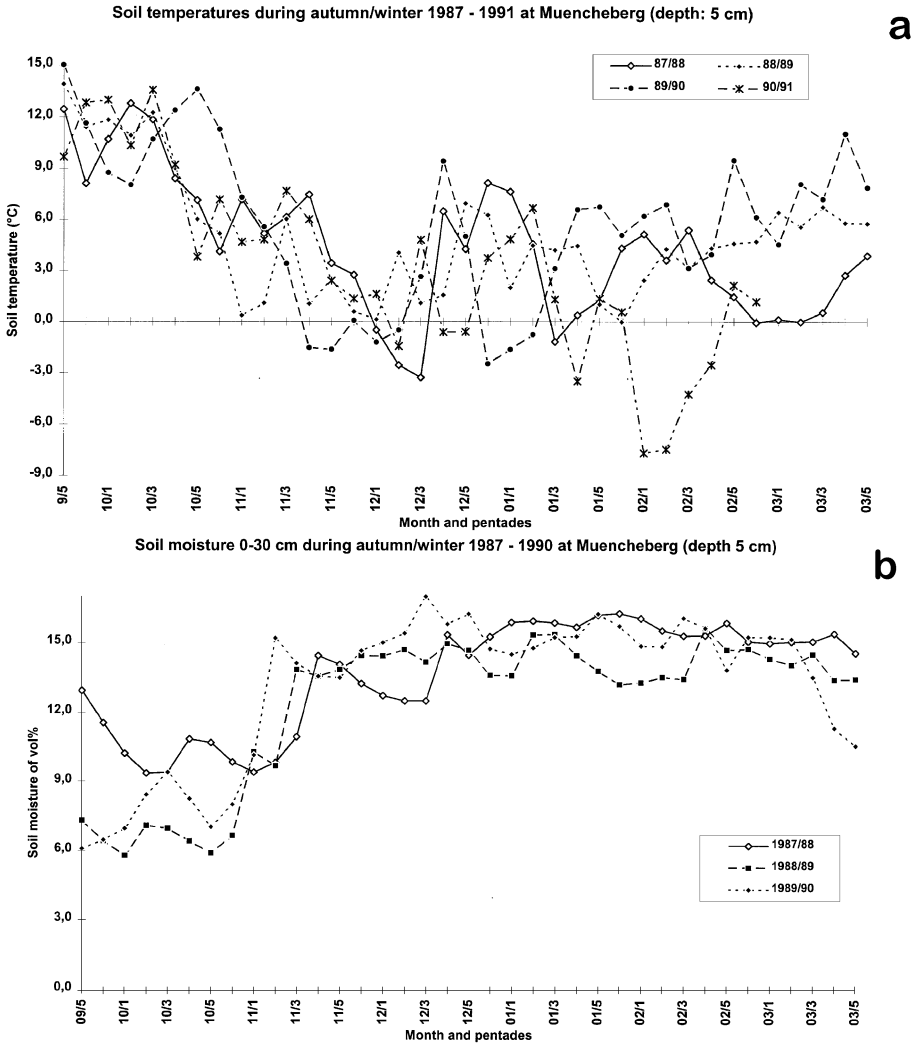

Figure 2a–b. Weather data for the autumn and winter months, average over 5 day intervals (pentades), in the years of field trials (loamy sand, albic luvisol) at the location Muencheberg (see Table 1); soil temperatures from 1987 to 1991 and soil moistures from 1987 to 1990 (1991 data were not available).

would allow evaluation of the suitability and consistency of performance of inoculated non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on plant growth. In this context, the effects of isolates used for inoculations on the early stages of wheat development were determined under soil moisture, temperature, and day-length conditions that simulated autumn weather in growth chamber experiments, and compared with the results of field trials over several years under real environmental conditions.

The results achieved in this work demonstrate that the shift from constant to variable environmental conditions in growth chamber experiments represents an important step towards more realistic simulations for the evaluation of the effects of fungal isolates of the *Gaeumannomyces/Phialophora* complex on the growth of wheat plants. These results should therefore be verified by testing the performances of non-pathogenic isolates under the environmental conditions of other regions with high rates of naturally occurring *Gaeumannonmyces* fungi, for example, in North Germany (Amelung and Focke, 1975), Central England (Deacon, 1973), and Western Australia (Sivasithamparam, 1993), as our results have shown that the effects of pathogenic and non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex on plant

growth are directly influenced by changes in the soil temperature and moisture conditions.

The effects of soil moisture on the disease are inconsistent. In some cases high infestation rates were found especially with high soil moisture levels (Schaffnit, 1930; Cook et al., 1972; Cannell et al., 1980; Catt et al., 1986). In other studies maximum infestation was found in soil with relatively little moisture (Winter, 1940; MacNish and Dodman, 1973; Amelung and Focke, 1975; Trolldenier, 1981; Grose et al., 1984; Wong, 1984; Douglas and Deacon, 1994). Whether or not this inconsistency is due to interrelations between soil moisture and soil substrate remains an open question (Wong, 1984). We assume that these contradictory results can be explained by the effects of more than one important simultaneously acting soil and environmental factor. Amelung and Focke (1975) conducted field experiments and Wong (1984) used laboratory experiments to study the combined effects of variable soil temperature and soil moisture levels on the activity of isolates of the *Gaeumannomyces/Phialophora* complex. Amelung and Focke (1975) found maximum take-all infestation on North Germany soils, in most cases after warm, dry winters. Because of profound differences in the experimental set-up, such results cannot be compared to these obtained in our study. Laboratory experiments of Wong (1984) included two relatively high soil temperature regimes (15 and 30 °C) and two soil moisture conditions (wet –0.3 Mpa and dry –10 Mpa). Interestingly, the behaviour of the tested pathogenic and non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex was similar to our results. For example, a non-pathogenic isolate of *Gaeumannomyces graminis* var. *graminis* stimulated plant growth in all cases, whereas another isolate of the same variety and all *Phialophora* isolates tested responded differently to changed soil moisture and soil conditions.

To work out prediction models for the occurrence and performance of pathogenic and non-pathogenic isolates of the *Gaeumannomyces/Phialophora* complex, several prerequisites for a description of the interaction processes have to be fulfilled. Specific field site characteristics, regional differences in the soil substrate, and weather have to be considered in detail, and it is necessary to evaluate the influences of these factors in comparison with other environmental and management parameters (e.g. crop rotation). Furthermore, the model has to include the effects of photoperiod, soil pH (Trolldenier, 1981), soil compaction (Glenn et al., 1987), soil C: N-ratio (Hoffmann and Schmutterer, 1983), activities of soil microorganisms (Winter, 1940), and land use systems (Steinbrenner, 1990).

A broad spectrum of isolates with different pathogenicities occur in the *Gaeumannomyces*/*Phialophora* complex that possess a close relationships, e.g. *P. graminicola* as an anamorph of *G. cylindrosporus* and *Phialophora* sp. (lobed hyphopodia) as an anamorph of *G. graminis* var. *graminis* (Balis, 1970; Scott, 1970; Deacon, 1973, 1974, 1976; Sivasithamparam, 1975; Wong, 1975; Lemaire et al., 1977; Wong and Southwell, 1980; Wong, 1981; Augustin, 1989, 1990, 1994). The identification of the fungal isolates by conventional methods such as pathogenicity tests on different hosts and the determination of morphological characteristics is slow and sometimes inconclusive (Ward, 1995). In addition, it could be assumed that varying performance under different test conditions may be caused by closely related isolates that were not differentiated previously, and have therefore been considered as one isolate or fungal strain. However, accurate isolate identification is now possible using molecular detection assays such as the polymerase chain reaction (PCR) (Ward, 1995). The use of PCR assays for isolates of *G. graminis*, allows prediction of the effects of a specific isolate on the host (Schesser et al., 1991; Henson et al., 1993; Augustin, 1994; Ward, 1995).

The effects of different environmental conditions on the interaction between isolates of the *Gaeumannomyces/Phialophora* complex and wheat can be explained by results from long-term field trials supported by the data of simulation experiments, and vice-versa. A consistent performance in the control of take-all by non-pathogenic isolates was achieved in field trials by Augustin (1994). Additional effects of the fungal inoculations on plant growth (in growth chambers and field experiments) are important, because further infections by naturally occurring pathogens on the experimental sites have to be taken into consideration. It is suggested that a reliable prognosis of the performance of non-pathogenic isolates under field conditions could be achieved in growth chamber experiments with wheat plants in the sensitive seedling development stage using simulated autumnal environmental conditions.

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