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The occurrence of *Mycosphaerella graminicola* and its anamorph *Septoria tritici* in winter wheat during the growing season

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Abstract

The disease septoria tritici blotch of wheat is initiated by ascospores of the teleomorph *Mycosphaerella graminicola* or pycnidiospores of the anamorph *Septoria tritici*. We report for the first time the presence of the teleomorph, *M. graminicola*, in Denmark. With the objective of elucidating the importance of the teleomorph for the development of septoria tritici blotch, data on the occurrence of fruit bodies of the anamorph (pycnidia) and the teleomorph (pseudothecia) stages were collected over three growing seasons. Pseudothecia were present in the springs, however, high numbers of pseudothecia compared to pycnidia were not observed until July, too late to influence the epidemic. On an individual leaf layer, pycnidia were observed well before pseudothecia. As the leaves aged, progressively higher proportions of fruit bodies were observed to be pseudothecia. The period from the appearance of pycnidia to detection of pseudothecia was estimated as 29–53 days. At harvest, high proportions of sporulating fruit bodies in the crop were pseudothecia, suggesting that the primary source of inoculum for new emerging wheat crops in autumn is likely to be ascospores.

Introduction

The fungus *Mycosphaerella graminicola* (anamorph *Septoria tritici*) causes septoria tritici blotch on wheat. Severe yield losses due to this disease are observed in wheat crops worldwide (Eyal et al., 1987). In Denmark, the importance of the disease has increased during the past decade, and it was the dominating disease on winter wheat in the years 1998–2000 (Pedersen et al., 2000).

The teleomorph, *M. graminicola*, was described in Europe in 1894 (Cunfer and Ueng, 1999), but it was not until 1972 that the connection between the anamorph *Septoria tritici*, and the teleomorph *M. graminicola* was discovered in New Zealand (Sanderson, 1972; 1976). Since then the teleomorph has been reported from many parts of the world including several countries in Europe (e.g. Kema et al., 1996; Scott et al., 1988).

Airborne ascospores have long been considered an important source of primary inoculum (Brown et al., 1978; Sanderson and Hampton, 1978; Shaw and Royle, 1989; Bathgate and Loughman, 2001), whereas during the growing season the epidemic was believed to be driven by short-range splash dispersed pycnidiospores. Reports of the presence of ascospores discharged from pseudothecia in the growing crop during spring and summer have changed this perception (Kema et al., 1996; Hunter et al., 1999). It has been suggested that the fungus may complete several sexual cycles during the growing season, and that airborne ascospore dispersal may play a larger role in the epidemic during the growing season than previously thought (Kema et al., 1996; Hunter et al., 1999). If airborne, as well as splash dispersed spores, are present in the growing crop it could have implications for the forecasting of disease (Hunter et al., 1999).

The objective of this study was to confirm the presence of the teleomorph, *M. graminicola*, in Denmark and to elucidate the importance of the teleomorph in relation to epidemics of septoria tritici blotch. To achieve this, development of the anamorph and teleomorph stages of the fungus was monitored in naturally infected winter wheat plots during three growing seasons, 1997/98, 1998/99 and 1999/00. In 1998/99 and 1999/00, the two stages of the fungus were quantified on individual leaf layers from December/January through to harvest in August.

Materials and methods

Plots of 50×50 m with susceptible winter wheat cultivars were monitored for the presence of the two stages of *M. graminicola*. The plots were treated according to normal agronomic practices, except application of fungicides was avoided.

1997/98

In 1997/98, the plot was sown with the susceptible cv. Brigadier. The previous crop was winter barley, and the area surrounding the plot was sown with winter barley. At regular intervals (approximately every three weeks) from December 1997 to August 1998, whole plants from the plot were sampled and examined for the presence of pseudothecia with ascospores. Ascospores were detected by letting the pseudothecia discharge according to the method described by Kema et al. (1996). Approximately 10 leaves per leaf layer, per sampling date, were soaked in tap water for 1 h and subsequently placed on moist filter paper in the lid of a Petri dish with water agar. The Petri dish was incubated on a laboratory bench upside down for a few hours or overnight. Discharged ascospores were isolated from the water agar, and transferred to PDA. Their identity was confirmed by observation of the typical colony development of *M. graminicola* on artificial medium. The pathogenicity of four ascospore-derived isolates from leaf 5 (flag leaf = 1) sampled on the 8 July 1998, was confirmed by inoculating wheat seedlings of the susceptible winter wheat cv. Sevin with an aqueous spore suspension. The seedlings were incubated in a growth chamber at 20 °C and with an 18-h light period, the first 48 h of incubation at 100% relative humidity. The seedlings were examined for pycnidia of *S. tritici* after 20 days. The last two samples from 30 July and 16 August 1998 were analysed as described below.

1998/99 and 1999/00

The plots were sited in commercial wheat fields grown with the susceptible cv. Ritmo. The previous crops were pea and oilseed rape for the fields used in 1998/99 and 1999/00, respectively. At regular intervals during each of the two seasons samples of 30 main tillers were collected randomly over the plot. In 1998/99, 15 samples were collected during the period from December to August. During winter, samples were taken once a month; in spring and summer sampling was done weekly. In the 1999/00 season seven samples were collected from January to August 2000, five of which were taken in the period May to August.

Percentage leaf area covered with fruit bodies of *M. graminicola* (pycnidia and pseudothecia) was assessed for each individual leaf layer on the 30 tillers. For 10 of the samples in 1998/99 and five of the samples in 1999/00, five leaves from leaf layers infected with septoria tritici blotch were chosen randomly from the whole sample for fruit body identification. Percentage leaf area covered with *M. graminicola* fruit bodies was assessed on these five leaves, and fruit bodies were picked off with a needle under a stereomicroscope from a number of randomly chosen microscope fields, along the length of the leaf. From the centre of each microscope field three to five fruit bodies were picked off. The fruit bodies were collected on a microscope slide in a drop of cotton blue (0.5% in a 1 : 1 : 1 mixture of lactic acid, glycerol and water), crushed and identified based on the morphology of the spores they contained. The fruit bodies found were allocated to the following three classes. (i) mature pycnidia of *S. tritici* with visible pycnidiospores, (ii) pseudothecia of *M. graminicola* with at least one mature ascus, (iii) not identified. This last class included exhausted and immature pycnidia (*S. tritici*) and pseudothecia (*M. graminicola*), and fruit bodies of other fungi. Collection of fruit bodies per leaf was continued until at least 30 fruit bodies had been collected, or until all the fruit bodies on the leaf had been collected. This gave a total of around 150 fruit bodies examined per leaf layer per sampling date. The identification of the teleomorph was based on colony morphology and pathogenicity of ascospore-derived isolates, as described above for the 1997/98 experiment. Ascospore-derived isolates were collected from leaf 6 sampled on the 9 July 1999, and from leaves 1, 2 and 3 sampled on the 23 August 1999, four isolates in total. For randomly chosen pseudothecia in different samples, the number of asci were counted, and

measurements of asci and ascospores were performed at 1000× magnification under the light microscope.

Results

The teleomorph of *M. graminicola* in Denmark was first observed in a sample from the 29 April 1998. During the rest of the season, discharge of ascospores from leaf samples was observed regularly, and by the end of the season ascospore discharge had been detected from all leaf layers from leaf 6 (flag leaf = 1) and above (Table 1). For selected sampling dates during the following two seasons, leaf layers displaying more than a few percent coverage with pycnidia were examined for the presence of pseudothecia. The lowest leaf layers examined were usually partly disintegrated and only part of the leaves remained. No leaf material of any significance was detected in the base of the crop. In 1998/99, pseudothecia were first detected on leaf 10 sampled on the 8th April, and with coverage of *M. graminicola* fruit bodies (pycnidia and pseudothecia) of 100%. Subsequently, pseudothecia were observed on successive leaf layers through the season ending with the flag leaf in August. In 1999/00, pycnidia and pseudothecia were not quantified during April and May; thus early detection below leaf 6 was not possible. Again, in this season, pseudothecia were detected on all subsequent leaf layers. Pseudothecia were only found on leaf layers where the average coverage with fruit bodies exceeded 38%, and where lesions had coalesced (Table 1). The only exception was leaf 5 on the 22 June 1999 where the proportion of pseudothecia was 2% on leaves with only 13% fruit body coverage.

In the first season, on the 16 August 1998, the proportion of *M. graminicola* fruit bodies (pycnidia and pseudothecia) assigned to the category mature pseudothecia, was 85%, 71%, 95% and 100% for leaf layers 1, 2, 3 and 4, respectively. Similar patterns in

Table 1. Mature *M. graminicola* pseudothecia as a proportion (%) of *M. graminicola* fruit bodies (pycnidia and pseudothecia) on individual leaf layers, in a winter wheat crop of cv. Brigadier in 1997/98 and cv. Ritmo in 1998/99 and 1999/00. Figures in parentheses for 1998/99 and 1999/00 are percent leaf area covered with fruit bodies on the five examined leaves

Date	Leaf layer										
	1 (flag)	2	3	4	5	6	7	8	9	10	11
1997/98[1]											
3 June					−[2]	−[2]					
15 June				−[2]	−[2]	+[3]					
8 July			−[2]	−[2]	+[3]						
30 July	76	76	96	100							
16 August	85	71	95	100							
1998/99											
16 December										0 (1)	
20 January										0 (12)	
8 April								0 (25)	0 (70)	1 (100)	
7 May								1 (86)			
21 May					0 (13)	0 (31)	1 (43)				
2 June					0 (25)	0 (43)	7 (70)				
22 June					2 (13)	13 (61)	38 (53)				
9 July				2 (44)	16 (38)	80 (80)					
30 July		27 (88)	24 (46)	56 (66)	79 (50)						
23 August	3 (91)	52 (73)	40 (70)	73 (77)	75 (73)						
1999/00											
6 January											0 (13)
8 March									0 (78)	0 (78)	
8 June				0 (22)	0 (70)	0 (89)					
27 June			0 (35)	9 (66)	63 (90)	67 (100)					
4 August	45 (100)	58 (100)	71 (100)	67 (100)							

[1]Samples were checked for ascospore discharge regularly from December 1997; ascospores were detected on the lower necrotic leaves from the 29 April.
[2]No ascospore discharge detected.
[3]Ascospore discharge detected.

appearance and proportions of pseudothecia and pycnidia were seen in the following two seasons. The most detailed data were collected in 1998/99 and showed that the proportion of *M. graminicola* fruit bodies, which were pseudothecia, increased over the lifetime of the individual leaf layers (Table 1). The result was a pattern where the proportion of pseudothecia at any given time usually decreased from lower to higher leaf layers. The proportion of pseudothecia reached final levels of more than 70–80% on leaves 4, 5 and 6. Pycnidia on a particular leaf layer always appeared well before pseudothecia (compare Tables 1 and 2). The fewer samples collected in 1999/00 suggested a similar pattern. The delay in days from the appearance of pycnidia to the appearance of pseudothecia was estimated for the four upper leaves in 1998/99 as 53, 29, 46 and 37 days for leaves 1, 2, 3 and 4, respectively. Since samples for assessment of fruit bodies were only taken approximately every three weeks these figures are inaccurate; however, they can be taken as a maximum delay.

Considering all leaf layers and the three categories of fruit bodies in 1998/99 and 1999/00 the same trend was observed as on individual leaf layers. The proportion of total fruit bodies identified as mature pseudothecia of *M. graminicola* increased over the season and the proportion of mature pycnidia decreased (Figure 1a,b). The proportion of pseudothecia did not reach levels comparable to the proportion of pycnidia until July. In 1998/99, the proportion of pycnidia was still 2.5 times higher than pseudothecia on the 9th July, but on the 30 July the two proportions were the same. In 1999/00, the proportion of pycnidia was twice as high as pseudothecia on the 27 June, but by the 4th August the proportion of pycnidia was considerably lower than the proportion of pseudothecia. The proportion of total fruit bodies assigned to the class not identified, i.e. they were not mature pycnidia of *S. tritici* or mature pseudothecia of *M. graminicola*, increased over the season from a few percent to about 80% in 1998/99 and to 60% in 1999/00 (Figure 1a,b); this reflects the development on the individual leaves. In the early samples from a particular leaf layer, practically all fruit bodies were identified as *M. graminicola* (pycnidia or pseudothecia), whereas in later samples a progressively larger proportion of the fruit bodies could not be identified (not shown).

The identification of fruit bodies was based on spore morphology and pathogenicity tests. The range in the size of asci was 24–60 × 7–25 μm with a mean of 38.8 × 10.8 μm, and for ascospores the range in size was 8–15 × 2.5–5 μm with a mean of

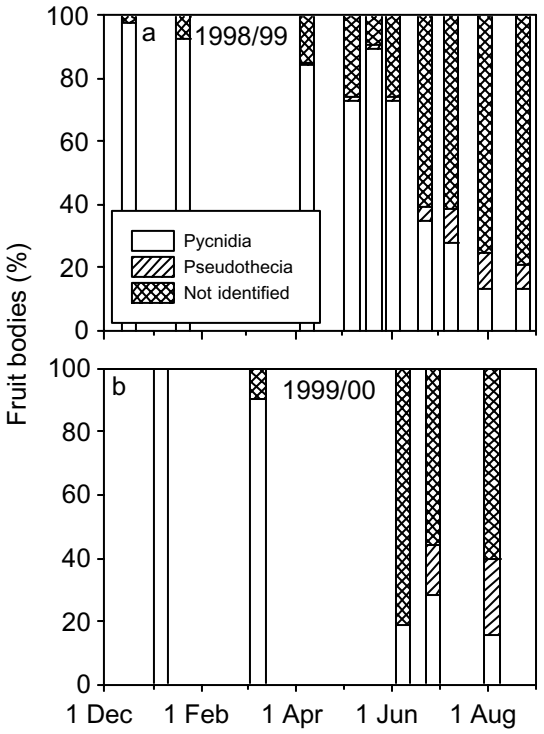

Figure 1. Fungal fruit bodies on leaves of a winter wheat crop of cv. Ritmo, in 1998/99 (a) and 1999/00 (b). The proportion of total fruit bodies examined is allocated to the three classes: mature pycnidia of *S. tritici*, mature pseudothecia of *M. graminicola* and fruit bodies not identified. Data collected from the individual leaf layers are pooled.

13.4 × 3.8 μm. These mean sizes agreed well with the observations of Sanderson (1976). The number of asci per pseudothecium was counted for 77 randomly chosen pseudothecia. The average number of asci per pseudothecium was 26, with a variation from 19 to 45. This gave an average of approximately 200 spores per pseudothecium, assuming that all asci were mature and that each held eight spores. The colony morphology of the ascospore-derived isolates on agar was typical of *M. graminicola* on artificial medium. All the tested isolates were pathogenic on susceptible wheat seedlings, producing the typical lesions of septoria tritici blotch with pycnidia exuding pycnidiospores in a cirrhus.

The disease severity measured as area covered with fungal fruit bodies reached high levels in each of the three seasons. In 1997/98, at the end of the growing season almost complete coverage of flag leaves with fruit bodies was observed (not shown). In 1998/99 and 1999/00, the epidemic started more slowly, but the final disease severity on the upper four leaves was high

Table 2. Percent leaf area covered with fruit bodies of *M. graminicola* on individual leaf layers (average of 30 leaves), in a winter wheat crop of cv. Ritmo in 1998/99 and 1999/00

Date	Growth stage	Leaf layer										
		1 (flag)	2	3	4	5	6	7	8	9	10	11
1998/99												
16 December	13										1	
20 January	22								1	4	8	
4 March	22								9	39	29	
8 April	23								18	76	98	
7 May	31						1	25				
21 May	37					7	19	65				
2 June	45				1	21	20					
14 June	57			1	4	12						
22 June	61			2	4	12						
1 July	65	1	4	16	26							
9 July	70	2	12	30	30							
17 July	77	17	31									
24 July	83	41	53									
1999/00												
6 January	23									0	7	13
8 March	25							1	31	71	77	
10 May	—				2	3	14					
8 June	—			1	18	85						
27 June	75	5	8	22	73							
16 July	—	51	74	85								

(Table 2). In both years the disease developed in parallel on successive leaf layers during the season, with the highest disease severity on the lowest leaves.

Discussion

Ascospores discharged from pseudothecia in left-over stubble have frequently been trapped from the air in autumn and winter, and connected to the primary infections in newly established wheat crops (Brown et al., 1978; Sanderson and Hampton, 1978; Bathgate and Loughman, 2001). This role for the ascospores is supported by the present study, where pseudothecia were available in large numbers at the end of the growing season. Ascospore discharge has also been found during the growing season in The Netherlands (Kema et al., 1996) and in England (Hunter et al., 1999). In these studies, no direct comparison was made between the amount of ascospore and pycnidiospore inoculum present in the crop, and it was thus not possible to estimate the influence ascospores may have on the secondary infections which occur during the growing season. The objective of the present study was to provide an estimate of the occurrence of both the teleomorph and anamorph stages of the fungus, and thereby clarify the influence of ascospores on the epidemic. To solve this problem an estimate of the number of infections initiated by ascospores and pycnidiospores, respectively, is needed. This would be very difficult and require extensive microscopy studies of leaves from naturally infected crops. An alternative would be to measure the amount of spores released in the crop. However, due to the different dispersal mechanisms of ascospores and pycnidiospores, a direct comparison of the number of spores in the crop by spore trapping is problematic. It was therefore decided to directly determine the numbers of fruit bodies producing the two types of spores in the crop. This method is independent of differences in dispersal mechanisms and infection efficiency between the two spore types. Sampling was performed in a winter wheat crop over three growing seasons starting in December when the first symptoms of septoria tritici blotch appeared and ending at harvest, with the majority of the sampling concentrated between May and August. However, sampling was limited in two of the three seasons 1997/98 and 1999/00; only in the 1998/99 season were all leaf layers sampled and examined for pseudothecia at least once.

The data showed that it was not until July that the number of pseudothecia reached a significant level compared to the number of pycnidia. With a

latent period in the field of 17–23 days (Shaw, 1990), ascospores produced at the end of July cannot contribute to the epidemic before harvest. A pycnidium, furthermore, holds several thousand spores (Eyal, 1971; Gough, 1978), whereas the pseudothecia collected during this study contained only a few hundred spores. Consequently, the vast majority of the inoculum present in the crop was pycnidiospores until the very end of the growing season, when no susceptible leaf tissue was available for infection. A similar conclusion was reached in Argentina, where ascospores and pycnidiospores were trapped in petroleum jelly on microscope slides (Cordo et al., 1999). It could be argued that the proportion of pycnidiospores and ascospores depends on environmental conditions in a specific year or in a specific wheat growing area, which would influence the severity and temporal dynamics of the disease. However, studies with a mathematical model showed the effect of ascospores on the progress of the epidemic to be very small (Eriksen et al., 2001). This was true even when unrealistic epidemiological parameters were chosen, favouring ascospores compared to pycnidiospores. An additional source of ascospores would be any crop debris left in the field from previous wheat crops. This is not relevant to this study as the monitored plots were in first year wheat crops established after ploughing, and consequently no crop debris was present. Any debris produced in the crop from leaves falling on the ground was very limited. However, in regions of no-till cropping and where wheat is grown after wheat, crop debris could be an additional potentially important source of ascospores.

There was a considerable delay from the end of the latent period, defined as the observation of sporulating pycnidia, to the observation of pseudothecia on a particular leaf layer. When this delay of 29–53 days is added to the latent period in the field of 17–23 days (Shaw, 1990), an estimate of the period from infection to the appearance of pseudothecia of 46–76 days is obtained. This estimate is in good agreement with field observations in the UK, where mature pseudothecia have been observed on flag leaves 75 days after flag leaf emergence (Hunter et al., 1999).

This study has demonstrated that pseudothecia occurred on successive leaf layers during the season. Similar results have been observed in England, where the first pseudothecia in an unsprayed winter wheat crop in 1997 were found on leaf 8 at the end of April, from which time pseudothecia appeared on progressively higher leaf layers during the season, reaching the flag leaf by mid July (Hunter et al., 1999). In The Netherlands, ascospore discharge from samples collected from a farmer's field in 1995 was found from early April through to the end of the growing season (Kema et al., 1996).

In the late samples in each of the three seasons, high proportions of pseudothecia compared to pycnidia were found; this could be a result of pycnidia being exhausted and therefore counted as unidentified fruit bodies, as the majority contained no spores, but had walls closely resembling those of sexual or asexual fruit bodies of *M. graminicola*. In Poland, second leaves were examined at growth stage 85 (Zadoks), and it was found that 9% of the leaf area infected with *M. graminicola* was occupied by pycnidia and 15% by pseudothecia (Glazek and Sikora, 1998).

The fact that pseudothecia were almost exclusively found on heavily diseased leaves with coalesced lesions, can be explained by the mating system of the fungus. The mating system is believed to be bipolar and heterothallic (Kema et al., 1996), and there are no reports of the involvement of microspores. Consequently, the two different mating types have to meet in the leaf for the initiation of a pseudothecium. Most lesions are apparently initiated by a single genotype (McDonald and Martinez, 1990), making it necessary for lesions to coalesce for the two mating types to meet. In the field pseudothecia will therefore appear later than pycnidia. In artificial infection experiments where the two mating types were inoculated on seedlings, the period from inoculation to the appearance of pseudothecia was estimated to be 35 days (Kema et al., 1996) and 84–132 days (Hunter et al., 1999). Considering that the two mating types in such experiments will come into contact almost immediately, the data of Hunter et al. (1999) suggest a surprisingly long period to the detection of pseudothecia compared to the field estimates. Maybe the initiation of pseudothecia is not just a response to the meeting of two different mating types, but also a response to environmental factors (Chamberlain and Ingram, 1997). The production of airborne spores in response to the exhaustion of resources would be a logical survival strategy.

This study has confirmed that the teleomorph of *M. graminicola* occurs in Denmark; this was not known at the outset of these investigations. The data collected over three seasons in first year wheat crops suggest that in such crops airborne inoculum is widely available in late summer and autumn. The data from the two latter seasons suggest that during spring and to the end of June, where airborne inoculum could influence

the severity of the epidemic, only few ascospores were produced in the crop and the majority of inoculum present during this period was pycnidiospores.

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References

Bathgate JA and Loughman R (2001) Ascospores are a source of inoculum of *Phaeosphaeria nodorum*, *P. avenaria* f. sp. *avenaria* and *Mycosphaerella graminicola* in Western Australia. Australasian Plant Pathology 30: 317–322

Brown JS, Kellock AW and Paddick RG (1978) Distribution and dissemination of *Mycosphaerella graminicola* (Fuckel) Schroeter in relation to the epidemiology of speckled leaf blotch of wheat. Australian Journal of Agricultural Research 29: 1139–1145

Chamberlain M and Ingram DS (1997) The balance and interplay between asexual and sexual reproduction in fungi. Advances in Botanical Research 24: 71–87

Cordo CA, Simon MR, Perelló AE and Alippi HE (1999) Spore dispersal of leaf blotch pathogens of wheat (*Mycosphaerella graminicola* and *Septoria tritici*). In: van Ginkel M and Krupinsky J (eds) Septoria and Stagonospora Diseases of Cereals: A Compilation of Global Research (pp 98–101) CIMMYT, Mexico, DF

Cunfer BM and Ueng PP (1999) Taxonomy and identification of *Septoria* and *Stagonospora* species on small grain cereals. Annual Review of Phytopathology 37: 267–284

Eriksen L, Shaw MW and Østergård H (2001) A Model of the effect of pseudothecia on genetic recombination and epidemic development in populations of *Mycosphaerella graminicola*. Phytopathology 91: 240–248 and Erratum Phytopathology 91: 519

Eyal Z (1971) The kinetics of pycnospore liberation in *Septoria tritici*. Canadian Journal of Botany 49: 1095–1099

Eyal Z, Scharen AL and van Ginkel M (1987) The Septoria Diseases of Wheat: Concepts and Methods of Disease Management, CIMMYT, Mexico

Glazek M and Sikora H (1998) The occurrence of *Septoria tritici* and its teleomorph *Mycosphaerella graminicola* in the region of Upper Silesia in 1996. Journal of Plant Protection Research 38: 23–29

Gough FJ (1978) Effect of wheat host cultivars on pycnidiospore production by *Septoria tritici*. Phytopathology 68: 1343–1345

Hunter T, Coker RR and Royle DJ (1999) The teleomorph stage, *Mycosphaerella graminicola*, in epidemics of septoria tritici blotch on winter wheat in the UK. Plant Pathology 48: 51–57

Kema GHJ, Verstappen ECP, Todorova M and Waalwijk C (1996) Successful crosses and molecular tetrad and progeny analysis demonstrate heterothallism in *Mycosphaerella graminicola*. Current Genetics 30: 251–258

McDonald BA and Martinez JP (1990) DNA restriction fragment length polymorphisms among *Mycosphaerella graminicola* (anamorph *Septoria tritici*) isolates collected from a single wheat field. Phytopathology 80: 1368–1373

Pedersen JB, Nielsen GC, Petersen PH, Kristensen H and Jensen JE (2000) Vintersæd. In: Pedersen CÅ (ed) Oversigt over Landsforsøgene (pp 17–101) The Danish Agricultural Advisory Centre, Århus, Denmark

Sanderson FR (1972) A *Mycosphaerella* species as the ascogenous state of *Septoria tritici* Rob. and Desm. New Zealand Journal of Botany 10: 707–710

Sanderson FR (1976) *Mycosphaerella graminicola* (Fuckel) Sanderson comb. nov., the ascogenous state of *Septoria tritici* Rob. apud Desm. New Zealand Journal of Botany 14: 359–360

Sanderson FR and Hampton JG (1978) Role of the perfect states in the epidemiology of the common *Septoria* diseases of wheat. New Zealand Journal of Agricultural Research 21: 277–281

Scott PR, Sanderson FR and Benedikz PW (1988) Occurrence of *Mycosphaerella graminicola*, teleomorph of *Septoria tritici*, on wheat debris in the UK. Plant Pathology 37: 285–290

Shaw MW (1990) Effects of temperature, leaf wetness and cultivar on the latent period of *Mycosphaerella graminicola* on winter wheat. Plant Pathology 39: 255–268

Shaw MW and Royle DJ (1989) Airborne inoculum as a major source of *Septoria tritici* (*Mycosphaerella graminicola*) infections in winter wheat crops in the UK. Plant Pathology 38: 35–43