MINIREVIEW

Ramularia collo-cygni: the biology of an emerging pathogen of barley

Dale R. Walters, Neil D. Havis & Simon J.P. Oxley

Crop and Soil Systems Research Group, Scottish Agricultural College, Edinburgh, UK

Correspondence: Dale R. Walters, Crop and Soil Systems Research Group, Scottish Agricultural College, King's Buildings, West Mains Road, Edinburgh EH9 3JG, UK. Tel.: +44 131 535 4020; fax: +44 131 535 4144; e-mail: dale.walters@sac.ac.uk

Received 30 August 2007; accepted 2 October 2007.
First published online 7 December 2007.

DOI:10.1111/j.1574-6968.2007.00986.x

Editor: Richard Staples

Keywords
Ramularia collo-cygni; barley; leaf spotting; rubellins.

Abstract

Ramularia collo-cygni is now recognized as an important pathogen of barley in Northern Europe and New Zealand. It induces necrotic spotting and premature leaf senescence, leading to loss of green leaf area in crops, and can result in substantial yield losses. The fungus produces a number of anthraquinone toxins called rubellins, which act as host nonspecific toxins with photodynamic activity. These toxins induce lipid peroxidation and are possibly the cause of the chlorosis and necrosis observed in leaves infected with *R. collo-cygni*. The fact that the fungus can remain latent in barley plants until flowering, coupled with its very slow growth *in vitro*, makes it difficult to detect in crops. As a result, the epidemiology of this pathogen remains poorly understood. However, the recent development of rapid and reliable PCR methods for specific detection of *R. collo-cygni* offers the prospect of increased understanding of its epidemiology and improved disease control.

Introduction

Ramularia collo-cygni is a pathogen of increasing importance on barley crops in Northern Europe (Sachs *et al.*, 1998; Pinnschmidt & Hovmøller, 2003; Oxley & Havis, 2004) and has also been reported recently on oats and wheat (Huss *et al.*, 2005). It is the cause of Ramularia leaf spot (RLS), a disease which occurs late in the season and is characterized by small necrotic lesions, usually with a yellow halo (Salamati & Reitan, 2006). Although RLS was first reported more than 100 years ago, with Cavara (1893) describing the pathogen associated with it as *Ophiocladium hordei*, it was not until the early 1980s that RLS began to attract serious scientific attention. However, it was often confused with necrotic spotting caused by abiotic factors and pathogens such as *Pyrenophora teres* (Sachs *et al.*, 1998). Nevertheless, RLS has been reported from crops across Europe, including Denmark (Pinnschmidt & Hovmøller, 2004), the Czech Republic (Minařiková *et al.*, 2004), Germany (Sachs, 2000), Austria (Huss *et al.*, 1987), Scotland (Oxley *et al.*, 2002), as well as New Zealand (Sheridan, 2000; Harvey, 2002). The rapid leaf senescence induced by RLS results in premature loss of green leaf area in crops and can lead to substantial yield losses (Huss *et al.*, 1992; Pinnschmidt & Hovmøller, 2004). For example, in the UK in 2004, average yield losses were 0.4 tonnes ha^{-1} and these were frequently associated with a loss in grain quality (Oxley, 2007).

The fact that *R. collo-cygni* has been recognized as a major pathogen of barley only relatively recently is due in large part to difficulties in isolating and identifying the fungus (Sutton & Waller, 1988; Frei & Gindrat, 2000; Sachs, 2004). However, the recent development of molecular probes for detection of *R. collo-cygni* (Havis *et al.*, 2006a; Frei *et al.*, 2007) is likely to have a significant impact on studies on the epidemiology and population biology of this pathogen. This review will examine the taxonomy, biology and life cycle of *R. collo-cygni* and look at what is known about the mechanisms by which it causes leaf spotting and premature senescence in leaves.

Taxonomy

Ramularia collo-cygni was not considered to be a 'typical' *Ramularia* species because of its curled conidiophores (like a swan's neck; Fig. 1) and conidia with eccentrically positioned scars (Braun, 1998; Crous *et al.*, 2000). Initially, therefore, it was considered distinct from *Ramularia* and thought to typify the genus *Ophiocladium* Cavara (Braun,

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

1998). The fungus was described as *Ophiocladium hordei*, but was transferred to the genus *Ramularia* by Sutton & Waller (1988) as *R. collo-cygni*. Its taxonomy and nomenclature can be summarized as follows:

Ramularia collo-cygni B. Sutton and J.M. Waller, *Trans Brit Mycol Soc* **90 (1):** 57 (1988).

≡ *Ophiocladium hordei* Cavara, 1893.

≡ *Ovularia hordei* (Cavara) Sprague, 1946.

≡ *Ramularia hordeicola* Braun, 1988.

In 2000, Crous *et al*. reported the results of phylogenetic analyses carried out on ITS-1, ITS-2 and 5.8S DNA sequence data from 46 species of *Mycosphaerella*, including three species with *Ramularia* anamorphs. This work showed that not only does *R. collo-cygni* cluster with other typical *Ramularia* species, but the teleomorph of *R. collo-cygni*, if it exists, is likely to be a species of *Mycosphaerella* (Crous *et al*., 2000). Interestingly, Braun (cited in Salamati & Reitan, 2006) reported the existence of *Asteromella*-like structures on barley leaves in close association with *R. collo-cygni* and suggested that these structures might represent the microsporidial state of the fungus. More recently, Salamati & Reitan (2006) obtained the *Asteromella* stage of *R. collo-cygni* from *in vitro* cultures of the fungus. These observations support the work of Crous *et al*. (2000) and the suggestions of Braun (2004) that the teleomorph stage of *R. collo-cygni* is likely to be a species of *Mycosphaerella*.

Life cycle of *R. collo-cygni*

Conidia of *R. collo-cygni*, in common with spores of most fungal pathogens of plants, require moisture for germination and early development on the leaf surface. Indeed, Huss (2004) found that dew on leaf surfaces was sufficient to trigger conidial germination and subsequent development. On leaves of a suitable host, germination and mycelial growth is rapid, with entry into the leaf through open stomata within 24 h (Sutton & Waller, 1988). Once inside the leaf, the fungus grows intercellularly, forming branched hyphae which colonize the mesophyll tissue (Sutton & Waller, 1988). Under controlled conditions, the first symptoms of RLS appear after 7 days (Huss & Sachs, 1998): brown to blackish brown spots, 1–2 mm long and usually sharply delineated by leaf veins (Fig. 2). Neighbouring leaf spots can coalesce to form larger dark areas. Once leaf spots appear, the remainder of the leaf becomes chlorotic and then necrotic, usually starting at the leaf tip and margins (Huss, 2004). These are typical symptoms of RLS and appear on spring and winter barley under field conditions, usually after heading. Fungal sporulation only occurs in necrotic tissue, with conidiophores emerging through stomata in caespituli of up to 15, from underlying stromata. As indicated above, the terminal part of each conidiophore is strongly curved (Fig. 1) (Sutton & Waller, 1988), with the apical region

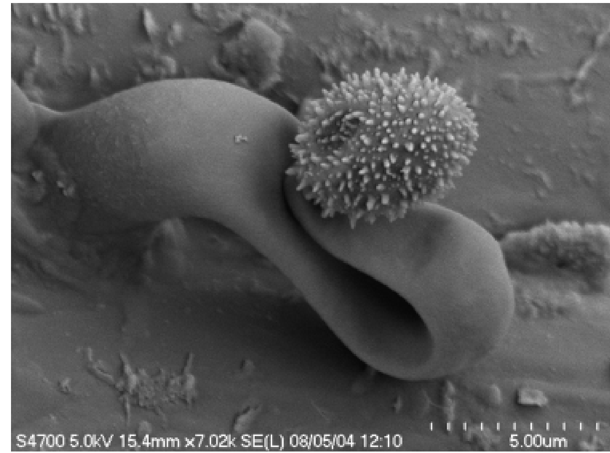

Fig. 1. Photomicrograph of the curled conidiophore of *Ramularia collo-cygni*. Note that it resembles a swan's neck or shepherd's crook.

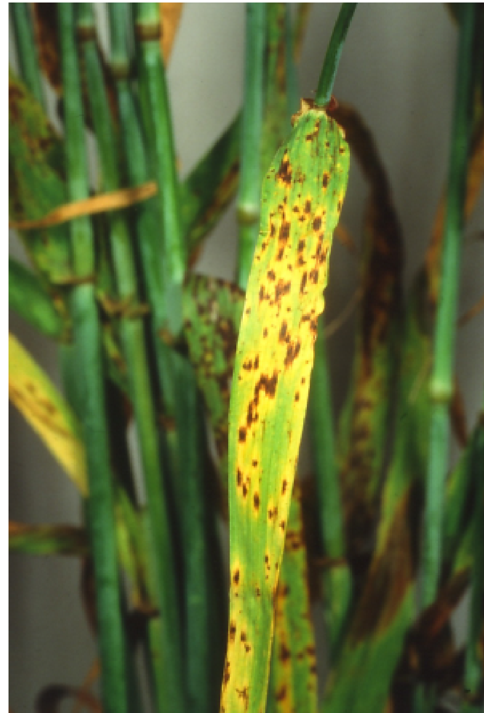

Fig. 2. Typical symptoms of *Ramularia* leaf spot (RLS) on barley leaves.

producing up to five conidia. *Ramularia collo-cygni* grows preferably, although not exclusively, on abaxial leaf surfaces and Huss (2004) estimates that a heavily infected leaf can produce up to 50 000 conidia.

There is considerable debate about the aetiology of the disease. Nevertheless, although RLS symptoms can start appearing in barley under field conditions early in the growing season (e.g. Harvey, 2002; Fig. 3), *R. collo-cygni* is known as a late season pathogen of barley, with typical RLS

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

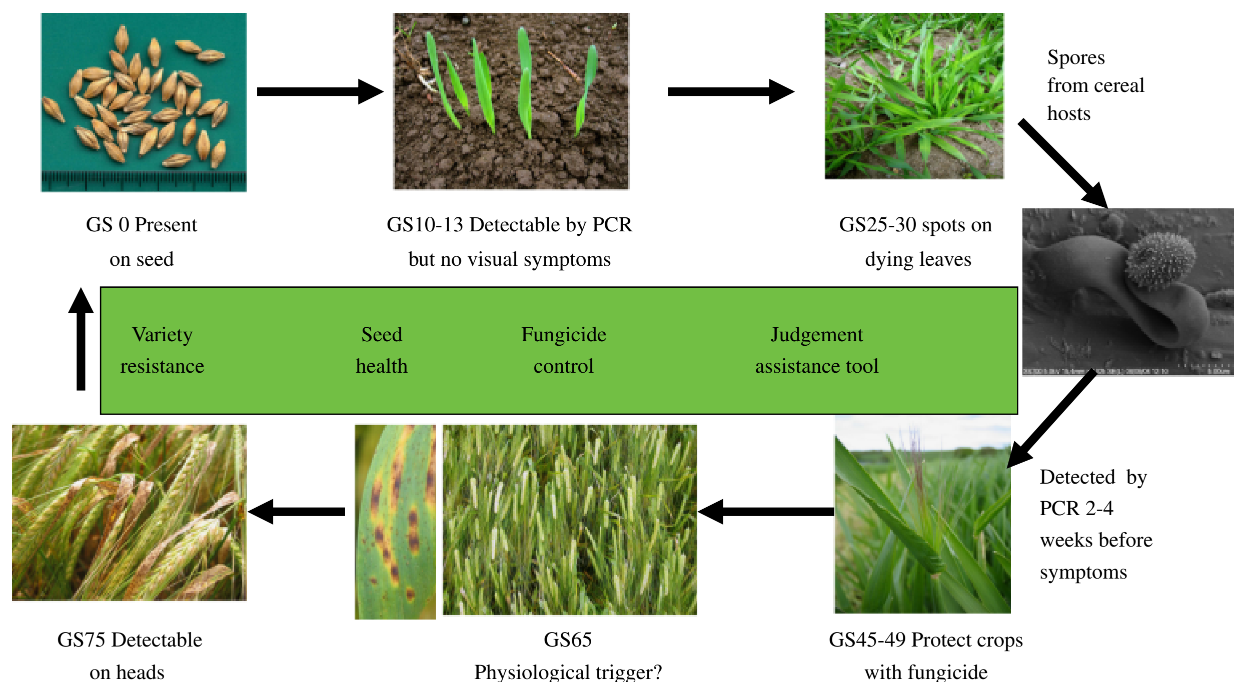

Fig. 3. Proposed life cycle of *Ramularia collo-cygni*. Inoculum sources include contaminated/infected seed and spores from other graminaceous hosts. Although symptoms of infection can be observed on leaves of young plants, the crop often appears symptomless until heading, when typical symptoms appear and the fungus sporulates profusely. The fungus can be detected on heads of barley, giving rise to seed contamination/infection. Understanding the life cycle fully is crucial for developing effective control measures. GS0 to GS75 represent stages on the Zadoks growth guide for barley.

symptoms appearing on foliage after emergence of the ear (Sachs *et al.*, 1998; Pinnschmidt & Hovmøller, 2003; Oxley & Havis, 2004; Fig. 3). During stem extension in barley, *R. collo-cygni* can survive as a saprophyte on the dead lower leaves (Huss, 2004). However, there is also evidence that it grows systemically and asymptomatically in the plant (Havis *et al.*, 2004; Salamati & Reitan, 2006), a conclusion confirmed by PCR-based detection methods (Havis *et al.*, 2006a, b). In these circumstances, symptom development and fungal sporulation appear to be triggered by the transition of the plant from vegetative to reproductive growth (Salamati & Reitan, 2006; Fig. 3). Whether environmental conditions have a role to play in the appearance of symptoms and fungal sporulation late in the season is not known.

It has been suggested that the symptoms on barley leaves induced by *R. collo-cygni* are dependent on light intensity (E. Sachs, unpublished results, quoted in Heiser *et al.*, 2003). Interestingly, recent work by Makepeace (2006) has shown that light intensity prior to inoculation exerts a significant effect on RLS. Plants grown under low light conditions before inoculation exhibited fewer RLS symptoms than did those grown under high light. However, increasing light intensity after plants were inoculated led to fewer RLS symptoms, suggesting that although light is required for the toxins produced by *R. collo-cygni* (rubellins; see below) to exert their effects, excessively high light intensities might have a negative effect on pathogenicity (Makepeace, 2006).

Ramularia collo-cygni may also be transmitted via seed (Fig. 3). Indeed, there is anecdotal evidence for a seed-borne phase for this pathogen (H. Huss, Versuchsstation Lambach-Stadl-Paura, Bundesamt für Agrarbiologie, Austria, pers. comm.). Support for seed transmission comes from recent work using a PCR-based diagnostic method developed for *R. collo-cygni*. Using this diagnostic tool, the pathogen was detected in barley grain samples harvested in 1999 and 2004 in Scotland (Havis *et al.*, 2006a, b). When seed carrying the pathogen was germinated, microscopic examination of seedling leaves revealed the presence of *R. collo-cygni* within leaves, although it was not present on the leaf surface (Havis *et al.*, 2006a; Havis *et al.*, unpublished results). As highlighted by Havis *et al.* (2006a), the existence of a seed-borne stage for *R. collo-cygni* will have serious implications for barley cultivation, as the fungus could be present in the majority of crops prior to symptom expression. However, as important as seed-borne transmission would be to barley crops, it is important to remember that there are a number of other possible sources of inoculum for this pathogen, including other graminaceous hosts such as oat, wheat, rye and couch grass (*Elymus repens*) (Huss, 2004; Salamati & Reitan, 2006) (Fig. 4). Recent work by Frei *et al.* (2007) has shown that winter barley is an important source

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

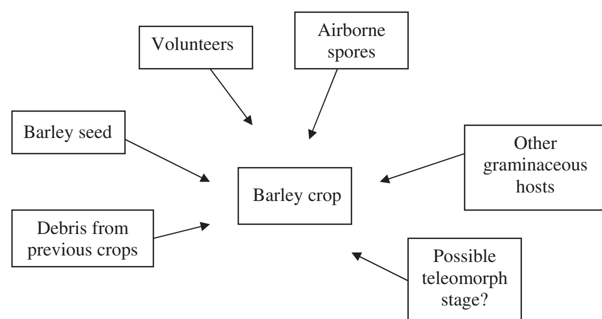

Fig. 4. Sources of inoculum of *Ramularia collo-cygni*.

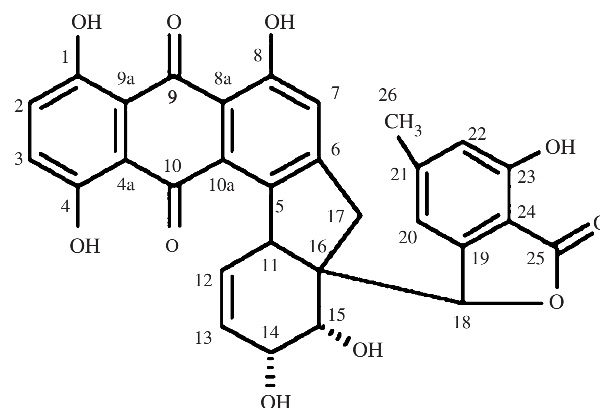

Fig. 5. Chemical structure of rubellin D.

of inoculum for spring barley and that the pathogen can spread from the winter to the spring crop.

It is important to note that the symptoms of RLS can easily be confused with those caused by abiotic stresses (physiological leaf spots, PLS; Wu & von Tiedemann, 2002) and by pathogens such as *Pyrenophora teres* (Sachs *et al.*, 1998). In fact, some authors have observed that *R. collo-cygni* was never the single cause of necrotic leaf spotting in experiments carried out under field conditions in Switzerland (Frei *et al.*, 2007). In this work, most necrotic leaf spotting was attributable to PLS. Reports such as these highlight the need for reliable means of detecting the fungus in plant material exhibiting symptoms of necrotic leaf spotting.

Toxin production by *R. collo-cygni*

In their work on *R. collo-cygni*, Sutton & Waller (1988) suggested that the staining reaction of mesophyll cells in the proximity of fungal hyphae might be due to production of a toxin. In fact, mycelium of *R. collo-cygni* growing on agar is coloured, the colour changing depending on the medium on which it is grown (Sutton & Waller, 1988; Salamati & Reitan, 2006). The purple colour of the mycelium led Heiser *et al.* (2003) to speculate that *R. collo-cygni* produces photoactive polycyclic aromatic toxins similar to cercosporin, produced by several species of *Cercospora*. They showed that *R. collo-cygni* produces a number of coloured metabolites, including an anthraquinoid identified as rubellin D (Fig. 5). When applied to barley leaves, rubellin D induced light- and concentration-dependent necrosis, and in a model system was shown to exhibit photodynamic activity, triggering the light-dependent production of reactive oxygen species (ROS), and to lead to the peroxidation of α-linolenic acid (Heiser *et al.*, 2003). Subsequent work demonstrated that rubellin D also induced the peroxidation of α-linolenic acid in barley and tobacco leaves, suggesting that it is a host nonspecific toxin (Heiser *et al.*, 2004). In fact, these workers showed that, in addition to rubellin D, *R. collo-cygni* also produces rubellins A, B, C and E (Fig. 5; Miethbauer *et al.*, 2003; Heiser *et al.*, 2004; Miethbauer *et al.*, 2006). In terms of relative ability to induce peroxidation of α-linolenic acid, rubellin A exhibited greatest activity, whereas rubellin E was ineffective (Miethbauer *et al.*, 2006). It seems likely that rubellin B, which is not soluble *in planta*, is produced first and is then converted to the more polar rubellin D, which possesses greater solubility *in planta* (Heiser *et al.*, 2004). Apparently, most of the rubellin in infected plant tissue is rubellin B (Miethbauer *et al.*, 2003).

The possibility that the rubellins might be involved in infection of host tissue by *R. collo-cygni* was ruled out by Miethbauer *et al.* (2003), as they were demonstrated to be host nonspecific toxins. Nevertheless, Heiser *et al.* (2004) proposed that they might be considered as pathogenicity factors. They suggest that rubellin production by the fungus results in oxidative stress, which in turn is involved in the formation of leaf spots. The fungus is then able to colonize the necrotic host tissue, while continued production of rubellins accelerates leaf necrosis. The early loss of green leaf area, coupled with reduced rates of photosynthesis, is likely to result in the premature ripening observed under field conditions (Heiser *et al.*, 2004).

Host resistance to *R. collo-cygni*

As indicated above, yield losses associated with infection of barley crops by *R. collo-cygni* can be substantial (Huss *et al.*, 1992; Pinnschmidt & Hovmøller, 2004). In fact, Harvey (2002) found that the correlation between disease severity and grain yield was non-linear, with low levels of infection exerting a major influence on grain yield. The disproportionate effect of infection on yield increases the importance of good disease control. Most barley varieties appear to be susceptible to the pathogen, although there is moderate resistance to *R. collo-cygni* in some varieties of both spring and winter barley (Pinnschmidt *et al.*, 2006). Some authors have reported that barley varieties carrying the *mlo* gene

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

conferring resistance to powdery mildew are the most susceptible to infection by *R. collo-cygni* (e.g. Reitan & Salamati, 2006). However, other work suggests that the *mlo* gene, in itself, does not increase susceptibility to *R. collo-cygni* and that the results obtained by others, e.g. Reitan & Salamati (2006), probably reflect differences in the genetic background of different varieties (Makepeace, 2006; Makepeace *et al*., 2007). Importantly, Makepeace (2006) found that varieties most resistant to *R. collo-cygni* under controlled conditions following seedling inoculation were most susceptible as adult plants under field conditions. These data suggest that there are different genes for resistance to *R. collo-cygni* at the seedling and adult plant stages or that some resistance genes are only expressed under specific field conditions (Makepeace, 2006). The detection of possible sources of resistance to *R. collo-cygni* in screening tests carried out under field conditions (Bistrich *et al*., 2006; Pinnschmidt *et al*., 2006) bodes well for the breeding of resistant varieties, although, clearly, this process is in its infancy. Currently, therefore, control of this pathogen is dependent on fungicides (Oxley *et al*., 2006).

Conclusions

Over the past 15 years, *R. collo-cygni* has become recognized as an important pathogen of barley. The reasons for this change in status are not known. However, it has been suggested that the introduction of barley varieties with increased susceptibility to abiotic stresses, coupled with decreased competition from other foliar pathogens as a result of improved control, are possible reasons for the increasing importance of *R. collo-cygni* (Salamati & Reitan, 2006). Understanding the causes of this relatively sudden appearance of *R. collo-cygni* as a major pathogen will be important in attempts to devise effective control measures. Further, it is clear from this brief review that the epidemiology of this pathogen is poorly understood. This is not surprising considering the slow growing nature of the fungus *in vitro* and the fact that it can remain undetected in plants until the reproductive phase starts. However, the recent development of rapid and reliable methods for detection of *R. collo-cygni* using PCR will make it easier to detect the pathogen in barley crops and should lead to increased information on its epidemiology. This is crucial for the development of robust systems for disease forecasting and improved disease control.

Acknowledgements

This work was funded through the Scottish Executive Environment and Rural Affairs Department workpackage on barley pathology (WP1.4).

References

Bistrich H, Breun J, Emmert G, Fleck A, Jaiser H, Kempe H & Lemmens M (2006) Screening for leaf spot resistance – results and impact on practical breeding. *Book of Abstracts of the First European Ramularia Workshop, Georg-August University Göttingen, Germany, March 2006* (von Tiedemann A, Schützendübel A & Koopman B, eds), p. 21 . http://wwwuser.gwdg.de/~rcc/index.htm.

Braun U (1998) *A Monograph of Cercosporella, Ramularia and Related Genera (Phytopathogenic Hyphomycetes)*, Vol. 2. IHW-Verlag, Eching, Germany.

Braun U (2004) *Ramularia collo-cygni* (*Ramularia* leaf blight of barley): taxonomy and phylogeny. *Meeting the Challenges of Barley Blights* (Yahyaoui AH, Brader L, Tekauz A, Wallwork H & Steffenson B, eds), pp. 370–375. *Proceedings of the Second International Workshop on Barley Leaf Blights, (ICARDA), Aleppo, Syria, April 2002*. http://www.icarda.org/Publications/Price_List/book3/Book3.html.

Cavara F (1893) Über einige parasitische Pilze auf dem Getreide. *Z Pflanzenkrankh* **3**: 16–26.

Crous PW, Aptroot A, Kang J-C, Braun U & Wingfield MJ (2000) The genus *Mycosphaerella* and its anamorphs. *Stud Mycol* **45**: 107–121.

Frei P & Gindrat D (2000) Le champignon *Ramularia collo-cygni* provoque une forme de grillures sur les feuilles d'orge d'automme et de graminées adventices. *Rev Suisse Agric* **32**: 229–233.

Frei P, Gindro K, Richter H & Schürch S (2007) Direct-PCR detection and epidemiology of *Ramularia collo-cygni* associated with barley necrotic leaf spots. *J Phytopathol* **155**: 281–288.

Harvey IC (2002) Epidemiology and control of leaf and awn spot of barley caused by *Ramularia collo-cygni*. *NZ Plant Prot* **55**: 331–335.

Havis ND, Piper SR, Oxley SJP & Langrell SRH (2004) Development of a PCR based identification and detection assay for *Ramularia collo-cygni* direct from barley leaf tissue. *Meeting the Challenges of Barley Blights* (Yahyaoui AH, Brader L, Tekauz A, Wallwork H & Steffenson B, eds), pp. 343–350. *Proceedings of the Second International Workshop on Barley Leaf Blights, (ICARDA), Aleppo, Syria, April 2002*. http://www.icarda.org/Publications/Price_List/book3/Book3.html.

Havis ND, Oxley SJP, Piper SR & Langrell SRH (2006a) Rapid nested PCR-based detection of *Ramularia collo-cygni* direct from barley. *FEMS Microbiol Lett* **256**: 217–223.

Havis ND, Pastok M, Pyzalski S & Oxley SJP (2006b) Investigating the life cycle of *Ramularia collo-cygni*. *The Dundee Conference: Crop Protection in Northern Britain 2006: Proceedings of the Conference Held at the West Park Conference Centre, University of Dundee, Scotland* (Heilbronn TD, ed), pp. 219–223, http://www.cpnb.org.

Heiser I, Sachs E & Liebermann B (2003) Photodynamic oxygen activation by rubellin D, a phytotoxin produced by *Ramularia*

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

collo-cygni (Sutton & Waller). *Physiol Mol Plant Pathol* **62**: 29–36.

Heiser I, Heß M, Schmidtke K-U, Vogler U, Miethbauer S & Liebermann B (2004) Fatty acid peroxidation by rubellin B, C and D, phytotoxins produced by *Ramularia collo-cygni* (Sutton & Waller). *Physiol Mol Plant Pathol* **64**: 135–143.

Huss H (2004) The biology of *Ramularia collo-cygni*. *Meeting the Challenges of Barley Blights* (Yahyaoui AH, Brader L, Tekauz A, Wallwork H & Steffenson B, eds), pp. 321–328. *Proceedings of the Second International Workshop on Barley Leaf Blights, (ICARDA), Aleppo, Syria, April 2002*. http://www.icarda.org/Publications/Price_List/book3/Book3.html.

Huss H & Sachs E (1998) *Ramularia*-Blattflecken-oder-Sprenkelkrankheit der Gerste. *Der Pflanzenarzt* **51**: 15–18.

Huss H, Mayrhofer H & Wetschnig W (1987) *Ophiocladium hordei* CAV. (Fungi imperfecti), ein für Österreich neuer parasitischer Pilz der Gerste. *Der Pflanzenarzt* **40**: 167–169.

Huss H, Mayrhofer H & Ingolič E (1992) *Ramularia collo-cygni* Sutton & Waller (Fungi imperfecti), ein wirtschaftlich beeunter Parasit der gerste in det Steiermark. *Mitt Naturwiss Ver Steiermark* **122**: 87–95.

Huss H, Liebermann B & Miethbauer (2005) Eine ernstzunehmende Krankheit auch an Hafer und Weizen: weitere Ausbreitung der Sprenkelkrankheit. *Der Pflanzenarzt* **9–10**: 8–10.

Makepeace JC (2006) The effect of the *mlo* mildew resistance gene on spotting diseases of barley. PhD Thesis, University of East Anglia, Norwich, UK.

Makepeace JC, Oxley SJP, Havis ND, Hackett R, Burke JI & Brown JKM (2007) Associations between fungal and abiotic leaf spotting and the presence of *mlo* alleles in barley. *Plant Pathology*. Doi: 10.1111/j.1365-3059.2007.01680.x.

Miethbauer S, Heiser I & Liebermann B (2003) The phytopathogenic fungus *Ramularia collo-cygni* produces biologically active rubellins on infected barley leaves. *J Phytopathol* **151**: 665–668.

Miethbauer S, Haase S, Schmidtke K-U, Günther W, Heiser I & Liebermann B (2006) Biosynthesis of photodynamically active rubellins and structure elucidation of new anthraquinone derivatives produced by *Ramularia collo-cygni*. *Phytochemistry* **67**: 1206–1213.

Minařiková V, Mařik P & Stemberková L (2004) Occurrence of a new fungal pathogen on barley, *Ramularia collo-cygni*, in the Czech Republic. *Meeting the Challenges of Barley Blights* (Yahyaoui AH, Brader L, Tekauz A, Wallwork H & Steffenson B, eds), pp. 360–364. *Proceedings of the Second International Workshop on Barley Leaf Blights, (ICARDA), Aleppo, Syria, April 2002*. http://www.icarda.org/Publications/Price_List/book3/Book3.html.

Oxley S (2007) Barley Disease Control, TN583, Scottish Agricultural College Edinburgh, UK. www.sac.ac.uk/consultancy/crops/publications/cropstechnotes/

Oxley SJP & Havis ND (2004) Development of Ramularia collo-cygni on spring barley and its impact on yield. *The Dundee Conference: Crop protection in Northern Britain 2004: Proceedings of the Conference Held at the West Park Conference Centre, University of Dundee, Scotland* (Heilbronn TD, ed), pp. 147–152, www.cpnb.org.

Oxley SJP, Havis ND, Sutherland KG & Nuttall M (2002) *Development of a Rationale to Identify the Causal Agent of Necrotic Lesions in Spring Barley and to Identify Control Mechanisms. HGCA Project Report No 282*. HGCA Publications, London, UK.

Oxley SJP, Havis ND & Hackett R (2006) Impact of fungicides and varietal resistance on *Ramularia collo-cygni* in spring barley. *Book of Abstracts of the First European Ramularia Workshop, Georg-August University Göttingen, Germany, March 2006* (von Tiedemann A, Schützendübel A & Koopman B, eds), p. 34. http://wwwuser.gwdg.de/∼rcc/index.htm.

Pinnschmidt HO & Hovmøller MS (2003) Ramularia, a new disease of barley – a review of present knowledge. *DJF Rep* **89**: 313–321.

Pinnschmidt HO & Hovmøller MS (2004) Ramularia-bladplet pa byg. (Ramularia leaf spots of barley). *Gron Viden, Markbrug* **290**, 6pp.

Pinnschmidt HO, Sindberg SA & Willas J (2006) Expression of Ramularia leaf spot resistance in barley cultivars and its relation to resistance against other diseases. *Proceedings of the ThirdInternational Workshop on Barley Leaf Blights, Edmonton, Canada, July 2006* (Turkington TK, Orr D & Xi K, eds), pp. 141–145.

Reitan L & Salamati S (2006) Field screening in Norway for resistance to *Ramularia collo-cygni* in old and new barley material. *Book of Abstracts of the First European Ramularia Workshop, Georg-August University Göttingen, Germany, March 2006*, (von Tiedemann A, Schützendübel A & Koopman B, eds), p. 20. http://wwwuser.gwdg.de/∼rcc/index.htm.

Sachs E (2000) Das Auftreten der *Ramularia*-Blattfleckenkrankheit an Gerste in Bayern 1999, verursacht durch *Ramularia collo-cygni* Sutton & Waller. *Nachrichtenbl Dt Pflanzenschutzd* **52**: 160–163.

Sachs E (2004) A 'new' leaf spot disease of barley caused by *Ramularia collo-cygni*: description, diagnosis and comparison with other leaf spots. *Meeting the Challenges of Barley Blights* (Yahyaoui AH, Brader L, Tekauz A, Wallwork H & Steffenson B, eds), pp. 365–369, *Proceedings of the Second International Workshop on Barley Leaf Blights (ICARDA), Aleppo, Syria, April 2002*. http://www.icarda.org/Publications/Price_List/book3/Book3.html.

Sachs E, Greil P, Amelung D & Huss H (1998) *Ramularia collo cygni* – a re-discovered barley pathogen in Europe. *Mitt BBA* **357**: 96–97.

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved

Salamati S & Reitan L (2006) *Ramularia collo-cygni* on spring barley, an overview of its biology and epidemiology. *Book of Abstracts of the First European Ramularia Workshop, Georg-August University Göttingen, Germany, March 2006* (von Tiedemann A, Schützendübel A & Koopman B, eds), p. 13 . http://wwwuser.gwdg.de/~rcc/index.htm.

Sheridan JE (2000) *Cereal Diseases 1999–2000 (Including Peas and Gooseberry Mildew). Disease Survey and Disease Control in the Waiarapa, New Zealand. Mycol. Plant Path. Rep. No. 37*. Botany Department, Victoria University of Wellington, Wellington, New Zealand.

Sutton B & Waller J (1988) Taxonomy of *Ophiocladium hordei* causing leaf lesions on *Triticale* and other *Gramineae*. *Trans Brit Mycol Soc* **90**: 55–61.

Wu YX & von Tiedemann A (2002) Evidence for oxidative stress involved in physiological leaf spot formation in winter and spring barley. *Phytopathology* **92**: 145–155.

Downloaded from https://academic.oup.com/femsle/article/279/1/1/498162 by guest on 19 April 2024

© 2007 Federation of European Microbiological Societies
Published by Blackwell Publishing Ltd. All rights reserved