IDENTIFICATION OF HOST RESISTANCE EFFECTIVE AGAINST THE BARLEY SPOT FORM NET BLOTCH PATHOGEN

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By
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In Partial Fulfillment
for the Degree of
MASTER OF SCIENCE

Major Department:
Plant Pathology

January 2014

Fargo, North Dakota
Title
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MASTER OF SCIENCE

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ABSTRACT

Spot form net blotch (SFNB) caused by *Pyrenophora teres f. maculata* is a major foliar disease of barley (*Hordeum vulgare* L.) worldwide. SFNB epidemics have recently been observed in major barley producing countries, suggesting that the local barley cultivars are not resistant and that virulence of the pathogen populations may have changed. Here we attempt to identify sources of resistance effective against diverse isolates of the SFNB pathogen. A total of 2062 world barley core collection accessions were phenotyped using isolates of this pathogen collected in the United States (FGO), Australia (SG1), New Zealand (NZKF2), and Denmark (DEN 2.6). Isolate-specific susceptibility was identified in several of the barley accessions tested, indicating variability in both pathogen virulence and host resistance/susceptibility. Collectively, only 15 barley accessions were resistant across all isolates tested. Future research will involve the characterization of host resistance, pathogen virulence, and the host-pathogen interaction associated with SFNB of barley.
ACKNOWLEDGEMENTS

I would like to acknowledge all the people who contributed directly or indirectly in my MS study and research activities. First of all, I am grateful to Dr. Timothy L. Friesen who welcomed me for graduate study under his supervision. I would like to thank him for his continuous support from starting of the research project till this date that involves a series of learning activities. I appreciate his advice and encouragement in building my professionalism in the academic and research fields. I would like to thank my academic advisor Dr. Robert Brueggeman for his support in both the academic and research fields. I am very grateful to my committee members Drs. Richard Horsley and Zhaohui Liu for their effort in my research work, academic activities, and manuscript reviewing. I would like to thank faculties, staffs and my colleagues in Plant Pathology & Plant Science department and NDSU campus. I am glad to have been part of the USDA/ARS, Northern Crop Science Research Laboratory (NCSL), Cereal Crops Research unit, so I would like to thank everyone for making a friendly and good research environment in our research unit.

I am thankful to our lab technician Danielle Holmes for teaching me new lab and greenhouse skills and providing me help during the entire research period. I would like to thank Dr. Jawahar Jyoti for helping me with my statistical analysis. I would also like to thank all members of the Friesen and Faris lab and my colleagues Prabin Tamang, Yuanyuan Gao, Yongmin Kim, Rachel Shjerve, Vaidehi Koladia, Gongjun Shi, and Jeff Geiser for their helping hands in my research. I’d also like to remember the city of Fargo, the NDSU community, NSA members, and all my friends for creating a good environment outside. Finally, I would like to thank my sweet family, relatives and friends in Nepal who provided me wishes for a success and warm love and support even from afar.
TABLE OF CONTENTS

ABSTRACT ...........................................................................................................................................iii

ACKNOWLEDGEMENTS .........................................................................................................................iv

LIST OF TABLES .....................................................................................................................................vii

LIST OF FIGURES ..................................................................................................................................viii

CHAPTER ONE. LITERATURE REVIEW .................................................................................................1

   Host (Barley) ........................................................................................................................................1

   Pathogen (*Pyrenophora teres f. maculata*) .........................................................................................2

   Life Cycle ...........................................................................................................................................3

   Infection and Disease Development ..................................................................................................3

   Host Pathogen Interaction .................................................................................................................4

   Pathogen Diversity .............................................................................................................................8

   Toxin Production ...............................................................................................................................9

   Fungal Genomics ...............................................................................................................................9

   Host Resistance ...............................................................................................................................10

   Literature Cited ...............................................................................................................................12
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Resistant barley accessions having average disease reaction scores of less than or equal to two across all four <em>P. teres f. maculata</em> isolates (FGO, SG1, NZKF2, and DEN 2.6) tested</td>
<td>31</td>
</tr>
<tr>
<td>2. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates FGO and SG1</td>
<td>36</td>
</tr>
<tr>
<td>3. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates FGO and DEN 2.6</td>
<td>37</td>
</tr>
<tr>
<td>4. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates FGO and NZKF2</td>
<td>39</td>
</tr>
<tr>
<td>5. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates SG1 and DEN 2.6</td>
<td>41</td>
</tr>
<tr>
<td>6. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates SG1 and NZKF2</td>
<td>43</td>
</tr>
<tr>
<td>7. Barley core collection lines showing a differential reaction between <em>P. teres f. maculata</em> isolates DEN 2.6 and NZKF2</td>
<td>45</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>SFNB disease rating scale</td>
<td>25</td>
</tr>
<tr>
<td>2.</td>
<td>SFNB disease progression</td>
<td>27</td>
</tr>
<tr>
<td>3.</td>
<td>Different lesion characteristics expressed by different barley lines 7 days post inoculation using the <em>P. teres f. maculata</em> isolate FGO</td>
<td>28</td>
</tr>
<tr>
<td>4.</td>
<td>Disease reaction score distribution of the four <em>P. teres f. maculata</em> isolates used</td>
<td>30</td>
</tr>
<tr>
<td>5.</td>
<td>Uniformly resistant barley lines seven days post inoculation using <em>P. teres f. maculata</em> isolates FGO, SG1, NZKF2 and DEN 2.6</td>
<td>47</td>
</tr>
</tbody>
</table>
CHAPTER ONE. LITERATURE REVIEW

Host (Barley)

Barley (*Hordeum vulgare* L.), is a self-pollinating diploid species with seven pair of chromosomes. The wild species of domesticated barley is thought to be abundant in grasslands and woodlands in the Fertile Crescent area of western Asia and northeastern Africa (Badr *et al.* 2000). Barley is classified in categories based on different physio-morphological characteristics. It is divided into two-rowed or six-rowed types, and shattering or non-shattering based on the nature of the spikes, and hull-less or hulled based on grain covering. The barley genome consists of seven pair of nuclear chromosomes (designated as 1H, 2H, 3H, 4H, 5H, 6H and 7H), and one mitochondrial and one chloroplastic chromosome with a total size of ~5000 Mbp (Mayer *et al.* 2012).

Barley is one of the major crops of the United States and the world (FAO STAT 2012). North Dakota is the leading state in barley production, producing more than one fourth of the US barley based on data from 2011, 2012 and 2013 (USDA-NASS 2013). Recently spot form net blotch (SFNB) has been identified in North Dakota (Liu *et al.* 2010) and popular cultivars from this region such as Tradition, Pinnacle, Robust, Lacey, and Celebration are susceptible (North Dakota barley council website available at http://www.ndbarley.net/?id=48, 30 October 2013). Various unpublished field data also documented that this area is facing significant losses from SFNB disease. Therefore, identification and genetic characterization of effective sources of host resistance and genetic characterization of pathogen virulence are both necessary for developing effective management strategies for this disease.
Pathogen (Pyrenophora teres f. maculata)

*P. teres* is an ascomycete fungus that belongs to the Dothideomycete class and the order Pleosporales. Other important plant pathogenic genera such as *Stagonospora*, *Cochliobolus*, *Ascochyta* and *Leptosphaeria* also fall under this order. *P. teres* is heterothallic in nature and therefore the sexual stage requires the two opposite mating types, MAT1-1 and MAT1-2, for sexual reproduction (Rau *et al.* 2005). There are two forms of *P. teres*, *P. teres* f. *maculata* and *P. teres* f. *teres*, which are genetically isolated and phylogenetically independent (Smedegard-Peterson, 1971; Rau *et al.* 2007). Although two forms are morphologically undifferentiated (reviewed Liu *et al.* 2011), the mating type locus sequences show that the two forms are distinct (Lu *et al.* 2010; Lu *et al.* 2013). The genetic distinction of the two forms indicates that the host pathogen interaction associated with each disease should be studied separately. Campbell *et al.* (2003) however, studied the in vitro mating of *P. teres* f. *maculata* and *P. teres* f. *teres* and found that the hybrid progeny retained their virulence and fertility over time and were genetically stable after two cycles of inoculation and re-isolation. They also reported that inoculation of hybrid progeny produced an intermediate symptom resulting in a jagged type spot. *P. teres* f. *teres* typically causes lesions having dark brown blotches in a net like structure (NFNB) while *P. teres* f. *maculata* causes dark brown round to elliptical lesions surrounded by a chlorotic halo (SFNB) (Smedegard Peterson, 1977).
Life Cycle

Both forms of *P. teres* follow a similar life cycle (McLean *et al.* 2009). The pathogen inoculum survives or overwinters in the stubble in the form of pseudothecia that harbor asci, each containing eight ascospores that mature and produce light brown colored ascospores (Webster, 1951; Mathre, 1997). Ascospores are actively discharged and dispersed by wind and rain splash, and act as a primary source of inoculum (Jordan, 1981). Conidia produced after the initial colonization serve as secondary inoculum and get dispersed by wind to neighboring fields to cause infection. The rate of an epidemic is influenced by environmental factors including relative humidity, leaf wetness, and temperature (Jordan, 1981; Mathre, 1997). In each growing season, a repeating secondary cycle can occur causing high disease severity if susceptible barley is grown under favorable environmental conditions. Eventually the pathogen colonizes the senescent tissue and produces pseudothecia that serve as overwintering structures that produce ascospores to initiate the cycle the following season.

Infection and Disease Development

Usually, infection and disease development occurs on the leaf; however, other plant parts including the stem and kernel can also be infected (reviewed in Liu *et al.* 2011). The infection process begins when conidia or ascospores, produced by over-wintering pseudothecia, land on the leaf surface and germinate under suitable temperature and moisture. The hyphae from the germ tube grow to varying lengths and form a swollen, club shaped appressoria, which acts as a penetration structure (Van Caeseele and Grumbles, 1979). The fungus penetrates the outer epidermal cell wall and the hypha develops into an intracellular vesicle, from which intracellular hyphae emerge and grow through the lower epidermal cells and then penetrate the mesophyll
tissue and start nutrient uptake from the host (Keon and Hargreaves, 1983). The susceptible host
cells start dying near or adjacent to the intracellular hyphae two days after inoculation (Keon and
Hargreaves, 1983). A chlorotic area starts to develop around the initial necrotic lesion and is
thought to be due to secretion of diffusible toxins or effectors disrupting the chloroplast or may
be due to the host defense response causing the death of adjacent cells via a program cell death
(PCD) mechanism like in other necrotrophic systems (Manning et al. 2009; Rasmussen et al.
2004 reviewed in Liu et al. 2011).

**Host Pathogen Interaction**

Plant disease results from the interaction of the host and the associated pathogen. The
plant possesses a recognition system against pathogens and the pathogen delivers effectors or
proteins to subvert plant defenses (Stukenbrock and McDonald, 2009). The specific host
pathogen interaction and associated level of plant immunity is different based on whether the
pathogen is biotrophic or necrotrophic. The model of the plant immune system often fits under
the zig-zag model (Jones and Dangl, 2006). Dangl and Jones (2001) and Jones and Dangl (2006)
defined a plant immunity model where the pathogen produces specific elicitors or pathogen
associated molecular patterns (PAMPs) that are recognized by pattern recognition receptors
(PRR), leading to downstream signaling, which induces resistance referred to as PAMP triggered
immunity (PTI). This PTI confers basal defense of the pathogen and is effective against many
non-adapted pathogens. Meanwhile, the pathogen also harbors virulence where new effectors are
secreted to break PTI, and induce susceptibility. Plants have also evolved a second line of
defense based on effector recognition. Classical resistance genes that often contain nucleotide
binding and leucine rich repeat (NB-LRR) domains are involved in recognition and signaling
defense resulting in effector triggered immunity (ETI) or race specific resistance. ETI is often associated with the hypersensitive response (HR) causing cell death that prevents the further growth of the pathogen. In the case of the biotrophic flax rust pathogen (*Melampsora lini*), Flor (1956) proposed a specific interaction for disease response that results from the expression of a plant resistance gene (R) and a pathogen avirulence gene (Avr). If the pathogen containing the avirulence factor (Avr) attempts to penetrate the host, this Avr gene product acts as an elicitor, that is recognized directly or indirectly by the plant R protein, activating a downstream signaling pathway that leads to resistance (Lauge *et al.* 1998).

Necrotrophic specialist pathogens produce and secrete necrotrophic effectors (synonym: host selective/specific toxins) that interact with dominant host susceptibility genes. The interaction of pathogen produced necrotrophic effectors and host produced gene products results in effector triggered susceptibility (ETS) (Friesen *et al.* 2007). In the case of a necrotrophic pathogen that feeds on dead tissue, PCD allows for further pathogen propagation (Stukenbrock and McDonald, 2009). This sort of susceptible reaction was validated based on the ToxA-*Tsn1* interaction, found in both the wheat-*P. tritici-repentis* and wheat-*S. nodorum* systems in which *Tsn1* confers sensitivity to ToxA produced by both pathogens and induces susceptibility (Friesen and Faris, 2010). This leads to a modification of the classical gene-for-gene model where instead of the presence of both effector proteins and host genes inducing an incompatible (resistant) interaction, the necrotrophic effector interacts with a dominant susceptibility gene in the host, resulting in a compatible (susceptible) interaction (Friesen *et al.* 2007, Friesen *et al.* 2008). Faris *et al.* (2010) cloned the *Tsn1* gene and found that it contained nucleotide binding site (NBS), leucine rich repeat (LRR) and serine/threonine protein kinase (S/TPK) domains and all three domains were required for ToxA sensitivity and disease susceptibility.
The host pathogen interaction model associated with both forms of *P. teres* has been studied; however, not enough is known to definitively describe how this interaction takes place. The interaction model in *P. teres f. teres* and barley is explained based on the nature of the resistance. Qualitative forms of virulence/avirulence have been shown in *P. teres f. teres* (Weiland et al. 1999; Beattie et al. 2007; Lai et al. 2007) possibly suggesting involvement of a gene-for-gene interaction, where single dominant resistant genes present in the host directly or indirectly recognize pathogen effectors, inducing a resistance response. Abu Qamar et al. (2008) identified two distinct loci segregating in a Rika × Komber doubled haploid population. In a separate cross using an F₂ population, Abu Qamar et al. (2008) showed that, opposite of a gene-for-gene type interaction, susceptibility was dominant. The presence of quantitative resistance (Robinson et al. 1997), the involvement of dominant susceptibility (Abu Qamar et al. 2008), and the presence of several minor virulence factors that accumulate to induce susceptibility (Sarpeleh et al. 2007) show that in addition to gene-for-gene type interactions there is also evidence for an inverse gene-for-gene model in the NFNB system.

The host pathogen interaction behind the *P. teres f. maculata* - barley pathosystem has not been fully worked out, with even less work being done on this system compared to the NFNB system; however, a review of the available literature helps in suggesting a model. Karki and Sharp (1986) studied the pathogenic variation in isolates of *P. teres f. maculata* by performing a cluster analysis of the mean disease rating of 14 isolates of *P. teres f. maculata* on 20 barley cultivars; they identified six distinct clusters. The Montana, USA and Mediterranean isolates used in this study showed distinct virulent or avirulent reactions across some cultivars, indicating an interaction in which specific pathogen effectors were interacting with specific genes present in the host, and showing that specific (likely gene-for-gene or inverse gene-for-
gene) interactions, similar to other necrotrophic specialists are present. Ho et al. (1996) performed genetic studies on a barley doubled haploid population using isolates of *P. teres f. maculata* and *P. teres f. teres*. They found that doubled haploid lines segregated in a 1:1 resistance to susceptible ratio when inoculated with *P. teres f. maculata*, indicating the involvement of a single resistant/susceptibility gene. While in an F₂ population derived from the same parental lines, this ratio was 9:7, which suggested the involvement of two complementary genes. Williams et al. (1999) used a barley doubled haploid population to evaluate resistance to *P. teres f. maculata* and found that resistance: susceptibility (R:S) segregated 1:1 and indicated that a single gene on the long arm of barley chromosome 7H, designated *Rpt4* was associated with SFNB disease in this population. Later, Williams et al. (2003) phenotyped five doubled haploid populations for seedling resistance and found that in three of the populations, resistance: susceptible segregation was nearly 1:1, indicating the involvement of a single gene conferring resistance/susceptibility, consistent with earlier results (William et al. 1999), while in the fifth DH population (VB9104 × Dash) the R:S ratio was 8:173, strongly suggesting the involvement of several susceptibility genes associated with disease.

Thus, the involvement of single genes (William et al. 1999; William et al. 2003), complementary genes (Ho et al. 1996), and multiple genes (William et al. 2003) has been shown to be associated with the SFNB interaction. Based on the evidence in the literature specific to the SFNB system and on research from other closely related necrotrophic specialist pathogens within the Pleosporales, including the genera *Cochliobolus, Pyrenophora*, and *Stagonospora* that produce necrotrophic effectors or host selective toxin, it is likely that *P. teres f. maculata* also uses necrotrophic effectors to induce disease susceptibility and at least partially follows an inverse gene-for-gene model. In addition, Sarpeleh et al. (2007) showed that like other
necrotrophic pathogens, *P. teres* f. *maculata* also produces host specific toxins, now referred to as necrotrophic effectors that are potentially involved in disease susceptibility. Genetic characterization of virulence from the pathogen side will provide a better understanding of this host-pathogen interaction.

**Pathogen Diversity**

Several studies suggest that the virulence associated with *P. teres* f. *maculata* is diverse. Karki and Sharp (1986) compared the virulence of *P. teres* f. *maculata* populations collected from the Mediterranean region and Montana, USA, using 20 differential barley lines and found that all of the pathogen isolates were either virulent or avirulent on some barley cultivars, while other barley lines showed a differential reaction between different isolates. Tekauz et al. (1990) identified 20 different pathotypes of *P. teres* f. *maculata* by evaluating a Canadian pathogen population using 12 differential barley lines. Gupta et al. (2012) studied the characterization and diversity of *P. teres* f. *maculata* in Australia and found that the pathogen population was highly diverse. Gupta et al. (2012) found an opposite reaction in barley line Betzes, where a pathogen population from Victoria, Australia induced a susceptible reaction and a pathogen population from Western Australia induced a resistant reaction, indicating different virulence spectra are present between these two pathogen populations within Australia. This shows the likely involvement of multiple interactions involving host genes and pathogen effectors. McLean et al. (2012) also reported a high degree of pathogenic variation in isolates of *P. teres* f. *maculata*, all suggesting that the development of barley cultivars with durable resistance will require a combination of multiple genes conferring a cumulative effect or the elimination of susceptibility genes. This form of durable resistance will be achieved from the selection of barley lines that
lacks susceptibility and further introgression of resistance genes into selected barley lines by breeding programs.

**Toxin Production**

The development of different types of disease symptoms is thought to be associated with the production of various toxins. Three toxins, Toxin A, Toxin B and Toxin C have been isolated from culture filtrates of *P. teres* that incite expression of both NFNB and SFNB symptoms, including water soaking, and necrosis and chlorosis of the leaf. However, the toxins have not been tied to the development of well-defined net or spot type symptoms in the leaf (Smedegard-Peterson, 1977; Friis *et al.* 1991; Weirgang *et al.* 2002). Sarpeleh *et al.* (2007) reported the identification of phytotoxic proteinaceous metabolites that were able to induce brown necrotic spots or lesions on susceptible barley cultivars while low molecular weight compounds induced yellow chlorotic lesions. The corresponding severity of the symptoms depended on the amount of the secreted toxins (Sarpeleh *et al.* 2007; Sarpeleh *et al.* 2008; Sarpeleh *et al.* 2009). Thus, in the case of *P. teres f. maculata*, several virulence factors including toxins are potentially important for inducing disease.

**Fungal Genomics**

Aragona *et al.* (2000) assumed a total of nine chromosomes present in *P. teres*, consistent with a genome size of at least 35 Mb. Cytological karyotyping analysis confirmed there were at least nine chromosomes present in *P. teres f. teres* (Ellwood *et al.* 2010). Ellwood *et al.* (2010) published the first genome assembly of *P. teres f. teres*, which showed that the total assembly size was approximately 41.95 Mbp and contained 11,799 gene models of greater than 50 amino
acids. The sequencing and genome assembly of *P. teres f. maculata* has not yet been published. However, the recent assembly of *P. teres f. maculata* shows approximately 11,000 total genes present in the *P. teres f. maculata* genome (Ellwood *et al.* unpublished data).

**Host Resistance**

Host resistance is an effective method to control SFNB of barley (Østergård *et al.* 2008). Probable sources of resistance include local landraces, wild barley, and cultivated accessions. Jana and Bailey (1995) found that an equal number of wild and cultivated barley accessions harbored resistance to SFNB based on the screening of west Asian barley lines and wild relatives using a Canadian *P. teres f. maculata* isolate. Very little research has been documented to recommend specific barley lines as effective resistance sources for SFNB, emphasizing the fact that resistance is rare. For instance, Williams *et al.* 1999 performed a screening for SFNB resistance in 96 Australian and Non-Australian lines, using a mix of southern Australian isolates, identifying four new sources of resistance including the feed cultivar Galleon and the breeding line WI2976. Tekauz *et al.* 1990 found few barley lines (CI 9214 and Heartland) were resistant across almost all western Canadian isolates (38 out of 42 isolates); a few lines (CI 5791 and CI 9820) were resistant across approximately half of the isolates, and some cultivars (Bonanza, Steptoe, Herta and Betzes) were resistant to only one isolate, while one barley line (BT 201) was susceptible to all isolates tested in this study.

Additionally, SFNB resistance can be growth stage specific. William *et al.* (2003) performed a seedling and field screening for SFNB resistance and found barley lines CI 9214 (Korean landrace), Dairokkaku (Japanese landrace), ‘Keel’, ‘Tilga’, VB9104 and Galleon to be resistant at both the seedling and adult plant stage, while some barley lines (e.g. WI 3141) were
resistant at the seedling stage only. Further, Mclean et al. (2012) evaluated the responses of 95 barley lines and cultivars to SFNB seedling and adult plant resistance in Australia and Canada. They found that only two lines were resistant to all isolates at the seedling stage, whereas 15 lines and cultivars were resistant to the two Canadian isolates and a mixture of Australian isolates at the adult stage.

Research has been carried out to explore the chromosomal location of SFNB resistance. Major and relatively minor SFNB resistance genes have been identified (reviewed in Liu et al. 2011). Williams et al. (1999) reported the presence of a major gene for SFNB seedling resistance on barley chromosome 7H designated as Rpt4. Williams et al. (2003) reported adult SFNB resistance on chromosomes 7H, 5H, and 4H using the same doubled haploid population used by Williams et al. (1999). Williams et al. (2003) also reported seedling resistance to SFNB on chromosome 7H, 3H and 1H. Friesen et al. (2006) identified a major QTL for seedling resistance to SFNB on chromosome 4H using a barley doubled haploid population and a pathogen isolate from New Zealand. Molnar et al. (2000) found that chromosome 2H was also associated with seedling resistance to SFNB using a Canadian isolate. Grewal et al. (2008) identified barley chromosome 4H and 7H as harboring SFNB seedling resistance to a Canadian P. teres f. maculata isolate and Manninen et al. (2006) reported SFNB seedling resistant on chromosome 5H against Finnish isolate. Thus, based on the above evidence it is concluded that resistance to P. teres f. maculata is present across several barley chromosomes and it is speculated that the nature of disease resistance to SFNB of barley is likely complex considering the fact that the sources of resistance can have major gene effects showing complete resistance in all stages of the crop or minor gene effects showing partial resistance in specific growth stages of the crop.
Characterization of both pathogen virulence and host resistance provides the best information to breeders to combat this disease.

**Literature Cited**


CHAPTER TWO. IDENTIFICATION OF HOST RESISTANCE EFFECTIVE AGAINST THE BARLY SPOT FORM NET BLOTCH PATHOGEN

Introduction

Barley (*Hordeum vulgare* L.) is one of the major crops of the United States and the world. Barley production faces several limiting factors including several diseases that have the potential to induce significant losses. Net blotch is a major foliar disease of barley and has two forms, net form net blotch (NFNB) caused by *Pyrenophora teres* f. *teres* and spot form net blotch (SFNB) caused by *P. teres* f. *maculata*. SFNB epidemics have been reported in major barley producing countries of the world including the United States, Canada, Australia, Denmark, Norway, and South Africa (reviewed in McLean *et al.* 2009 and Liu *et al.* 2011). SFNB yield losses have been reported up to 44% in Australia (Khan 1989; Jayasena *et al.* 2007). An increase in SFNB has recently been observed in the Northern Great Plains of the United States (Liu *et al.* 2010). The increases in disease epidemics in these areas are likely due to shifts in the virulence within the pathogen population, which are likely in response to changes in resistance/susceptibility in the prevalent cultivars grown.

Disease management tactics for SFNB consist of fungicide application, inoculum reducing cultural practices, and the introgression of resistance into popular cultivars (McLean *et al.* 2012; Østergård *et al.* 2008). Very little research has been documented to recommend specific barley accessions as effective resistance sources for SFNB. William *et al.* (1999) evaluated 96 Australian and international accessions for SFNB resistance using a mix of south Australian isolates, identifying only a few resistant barley accessions. Likewise, Mclean *et al.* (2012) evaluated the responses of 95 barley accessions and cultivars to SFNB seedling and adult plant resistance in Australia and Canada and found that only two were resistant to all isolates tested,
whereas 15 accessions, including cultivars, were resistant to the Canadian isolates tested and a mixture of Australian isolates at the adult plant stage. Gupta et al. (2012) also studied the response of barley accessions to *P. teres f. maculata* and found that six were resistant across most of the western Australian isolates tested. In the current research project we are using the barley core collection (BCC), which consists of a diverse set of 2062 accessions selected based on a sampling of the country of origin (available at http://www.ars-grin.gov/cgi-bin/npgs/html/eval.pl?281, 07-26-2013) to represent the global genetic diversity of cultivated barley and barley landraces, to identify SFNB resistance.

*Pyrenophora teres f. maculata* is a sexually reproducing fungus that is pathogenically variable within and between the barley growing regions (Karki and Sharp, 1986; Tekauz, 1990; Arabi et al. 1992; Gupta et al. 2001). A given source of resistance may be effective only towards a specific pathotype and may be susceptible to other pathotypes from other regions. Karki and Sharp (1986) compared the virulence of *P. teres f. maculata* populations collected from the Mediterranean region and Montana, USA, using 20 differential barley accessions; that found that approximately half of the accessions showed a differential response. Tekauz et al. (1990) identified 20 different pathotypes of *P. teres f. maculata* by evaluating a Canadian pathogen population using 12 differential barley genotypes. Gupta et al. (2012) studied the diversity of *P. teres f. maculata* in Australia and found that the pathogen population was highly diverse. Gupta et al. (2012) also found an opposite reaction in barley cultivars Betzes, where a pathogen population from Victoria induced a susceptible reaction and a pathogen population from Western Australia induced a resistant reaction, showing different virulence spectra was present between *P. teres f. maculata* populations within Australia. Collectively, these studies
indicated that the virulence of *P. teres* f. *maculata* was complex and needed further investigation before we could have confidence in the durability of any source of resistance.

The nature of host resistance involved in the SFNB interaction is not fully understood. Previous studies have reported involvement of single genes (William *et al.* 1999; William *et al.* 2003), complementary genes (Ho *et al.* 1996) and multiple genes (William *et al.* 2003) in the SFNB interaction. Additionally, resistance has been mapped to several barley chromosome arms and in some cases the resistance has been shown to be only effective at specific growth stages (reviewed in Liu *et al.* 2011).

The objective of this study was to identify barley lines that harbored high levels of SFNB resistance effective against a geographically and pathogenically diverse set of *P. teres* f. *maculata* isolates to be used in population development aimed at the characterization of SFNB resistance, as well as in germplasm and cultivar development.

**Materials and Methods**

**Plant materials**

A total of 2062 accessions of barley were evaluated for resistance to spot form net blotch (SFNB) (Appendix Table 1). This collection, referred to hereafter as the barley core collection (BCC), is made up of barley accessions representing 10% of the core set within the cultivated *H. vulgare* chosen based on country of origin (USDA, ARS, National Genetic Resources Program. *Germplasm Resources Information Network - (GRIN).* National Germplasm Resources Laboratory, Beltsville, Maryland. Available at http://www.ars-grin.gov/cgi-bin/npgs/html/eval.pl?281) (26 July 2013). The BCC was obtained from Harold Bockelman at
the USDA-ARS Small Grains Collection in Aberdeen, Idaho. Barley lines CIho 14219 and PI 67381 were used as resistant checks and Robust as a susceptible check.

**Disease evaluations**

All 2062 barley lines were evaluated using four *P. teres* f. *maculata* isolates including FGOB10Ptm-1 (FGO) collected in North Dakota, USA (from our collection), SG1 collected in Western Australia (obtained from Richard P. Oliver, Curtin University Perth Western Australia), NZKF2 collected in New Zealand and DEN 2.6 collected in Denmark (NZKF2 and DEN 2.6 isolates were obtained from Brian Steffenson, University of MN, USA). These isolates were chosen due to their different geographical distribution and therefore likely harbored different virulence.

The 2062 BCC lines were divided into 35 blocks; each block contained 60 barley accessions that fit into one rack surrounded by a border row of Robust barley to reduce any edge effect. Three barley seeds per line per replicate were sown into a single cone containing Metro mix soil (Sun Gro Hort. Co., USA). Plants were grown in the greenhouse until inoculations. Cones of one week old seedlings were fertilized with approximately 2 g of Osmocote controlled release fertilizer (Scotts, Marysville, OH, USA) having 15:9:12 NPK content. Barely accessions were inoculated as previously described by Friesen *et al.* (2006). Briefly, dried fungal mycelial plugs were placed in Petri plates containing V8-PDA media (150ml V8 juice, 10g difco PDA, 3g CaCO3, 10g agar, and 850ml distilled water). The plates were incubated in the dark at room temperature for 5 d and then subjected to 24 h continuous light at room temperature followed by another 24 h in the dark at 15°C to enhance sporulation. Conidia were harvested by scraping the surface of the plates with a sterile inoculating loop and the conidial concentration was adjusted to
2000 conidia/ml. Before inoculation, Tween 20 was applied at 2 drops/ 100 ml to enhance uniform distribution of the spores and adherence to the leaf surface. Two week old seedlings were spray inoculated to just before runoff using an air sprayer at 15-20 psi. Following inoculation, plants were incubated in a mist chamber for 22 - 24 h at 100% relative humidity under 24 h light to facilitate infection. The inoculated plants were then placed in a growth chamber under a 12 h photoperiod for 6 d at 21°C.

Disease reactions were evaluated 7 d post inoculation using a 1-5 rating scale (Figure 1). This rating scale categorizes the disease reaction based on lesion size and characteristic (Figure 1). Three seedlings planted in a single cone were evaluated collectively as one replicate. Plants having approximately equal amounts of two reaction types were given an intermediate rating (e.g. equal amounts of reaction type 2 and 3 resulted in a 2.5 rating). The overall experiment consisted of three replicates.
Figure 1. SFNB disease rating scale. Disease reactions were scored on a 1 (top) to 5 (bottom) reaction type scales. Two leaves are shown for each reaction type. A disease reaction type of 1 (resistant) consisted of small pinpoint lesions with no surrounding tan necrosis or yellow chlorosis, 2 consisted of pin point lesions with a small amount of necrosis and/or chlorosis around the penetration point, 3 consisted of necrotic or chlorotic lesions of 2-3 mm in size with little or no coalescence of the lesions, 4 consisted of necrotic and chlorotic lesions of greater than 3mm in diameter with moderate amounts of coalescing between lesions and covering less than 70% of the leaf area, and 5 consists of necrotic or chlorotic lesions coalescing and covering greater than 70% of the leaf area.
Results

Disease progression and phenotypes

Since little information has been reported on the progression of SFNB disease induced by
*P. teres f. maculata*, we evaluated disease progression in a single susceptible barley cultivar
(Tradition) with a single *P. teres f. maculata* isolate (FGO) (Figure 2). Additionally, using the
2062 accessions in the barley core collection we identified disease reactions on several
accessions that showed phenotypic differences (Figure 3) including combinations of necrosis and
chlorosis as well as regular and irregular lesion shapes. This allowed us to best be able to identify
a standard disease reaction type scale to evaluate levels of resistance/susceptibility across
different barley backgrounds.

For disease progress, disease was evaluated visually on the fully expanded secondary leaf
(approximately 14 d old seedlings). Leaves were cut and photographed at 24 h intervals until the
7th day (Figure 2). At one-day post inoculation (dpi), the inoculated leaves had a water soaked
appearance where the fungus had initiated penetration but no yellow or brown necrosis had
developed. At two dpi, diffuse chlorosis was beginning to develop and at three dpi, lesions were
becoming more distinct but continued to grow. Between four and six dpi the lesion size
expanded slightly but after six days, lesion size changes were not obvious. Therefore, disease
reaction types were evaluated at seven dpi when the lesion size had become static but before leaf
senescence. When evaluating the BCC, several different phenotypes were identified. Several of
these lesion phenotypes are presented in Figure 3. These phenotypes included various forms of
necrosis (Figure 3 A, C) and chlorosis (Figure 3 B) and combinations of the two (Figure 3 D, E,
Most commonly, susceptible reactions were displayed as circular to oval lesions that consisted of light brown to brown necrosis similar to the leaves in Figure 3 A and C.

Figure 2. SFNB disease progression. Disease progression was from 1 day to 7 d post inoculation using the *P. teres* f. *maculata* isolate FGO inoculated on the susceptible barley cultivar Tradition.
Figure 3. Different lesion characteristics expressed by barley lines 7 days post inoculation using the *P. teres f. maculata* isolate FGO. The top barley line (leaf A and C) shows necrosis, leaf B shows chlorosis, leaf D, E and F shows combination of both necrosis and chlorosis. Leaf A, B, and C have circular to elliptical lesions while D, E and F have elongated/irregular type lesions.

**Numerical disease reaction type scale**

Based on the disease progress observed in the previous section, disease reaction types were evaluated at 7 dpi based on a 1-5 reaction type scale where 1 was the most resistant and 5 was the most susceptible (Figure 1). Due to the differences identified in lesion types across the BCC, we based this disease scale primarily on lesion size and disease coverage on the leaf. A disease reaction type of 1 (resistant) consisted of small pinpoint lesions with no surrounding tan necrosis or yellow chlorosis. A disease reaction type of 2 (moderately resistant) consisted of pinpoint lesions with a small amount of necrosis and/or chlorosis around the penetration point. A disease reaction type of 3 (moderately susceptible) consisted of necrotic or chlorotic lesions of 2-3 mm across with little or no coalescence of the lesions. A disease reaction type of 4 (susceptible) consisted of necrotic and chlorotic lesions of greater than 3mm in diameter with moderate amounts of coalescing between lesions and covering less than 70% of the leaf area. A
disease reaction type of 5 (highly susceptible) consisted of necrotic or chlorotic lesions coalescing and covering greater than 70% of the leaf area.

**Pathogen virulence**

One of the objectives of this study was to identify barley accessions that showed a differential response among the four isolates used in this study for use in characterization of the genetics of pathogen virulence. When using a differential cutoff of 1.8, thirteen accessions showed a differential reaction between FGO and SG1 with twelve of those being more susceptible to FGO than to SG1 and only one being more susceptible to SG1 than FGO. Similarly, forty-two accessions showed a differential reaction between FGO and NZKF2 and twenty-seven accessions showed a differential reaction between FGO and DEN 2.6 with only one and five of those being more susceptible to NZKF2 and DEN 2.6, respectively. When comparing SG1 with NZKF2 and DEN 2.6, SG1 showed higher virulence on thirty-seven and twenty-nine accessions respectively, with NZKF2 and DEN 2.6 showing higher virulence to SG1 on only eight and ten accessions, respectively. When comparing NZKF2 and DEN 2.6, three lines showed a differential reaction with all three accessions being more susceptible to DEN 2.6.

**Host line responses and identification of resistant lines**

The disease score patterns observed were distributed in bell shaped pattern across the BCC with each of the four *P. teres* f. *maculata* isolates. The disease score reaction was categorized into five groups based on a numerical disease reaction; 1 to less than 1.5, 1.5 to less than 2.5, 2.5 to less than 3.5, 3.5 to less than 4.5 and 4.5 to 5. We found that only a few barley accessions fell under the resistant extreme (< 1.5) or the susceptible extreme (> 4.5), with most
of the accessions falling into an intermediate range of reaction types creating a bell shaped
distribution (Figure 4). Out of the 2062 barley accessions evaluated, only 50 showed an average
disease reaction of less than 2 using the FGO isolate, similarly only 79, 182 and 244 accessions
showed average disease reactions of less than 2 to SG1, DEN 2.6 and NZKF2, respectively. Only
12, 21, 42 and 66 accessions showed average disease reactions of 1 to less than 1.5 with FGO,
SG1, DEN 2.6 and NZKF2 isolates, respectively. Additionally, only 15 accessions showed a
disease reaction of less than or equal to 2 for all four isolates tested (Table 1).

![Disease reaction score distribution](image)

Figure 4. Disease reaction score distribution of the four *P. teres f. maculata* isolates used. Few
barley accessions are highly resistant or highly susceptible with most of the accessions showing
an intermediate reaction for each isolate resulting in a bell shaped curve.
Table 1. Resistant barley accessions having average disease reaction scores of less than or equal to two across all four *P. teres f. maculata* isolates (FGO, SG1, NZKF2, and DEN 2.6) tested.

<table>
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<th>Barley Accession</th>
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<th>Row type*</th>
<th>Accession type*</th>
<th>FGO</th>
<th>SG1</th>
<th>NZKF2</th>
<th>DEN 2.6</th>
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<td>PI 67381</td>
<td>Turkistan</td>
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<td>1.0</td>
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<td>Landrace</td>
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<td>1.5</td>
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<td>1</td>
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<td>1.5</td>
<td>2</td>
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<td>PI 84311</td>
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</table>

* Row type and accession type data were obtained from The Triticeae Tool Box (available at http://triticeaetoolbox.org/). Barley accessions were ordered based on average disease reaction from top to bottom respectively.
Discussion

Disease development and disease reaction characteristics

The development of the SFNB disease results from the infection process carried out by the pathogen *P. teres* f. *maculata*. The infection process includes the attachment of the spore to the leaf surface followed by spore germination, appressoria and penetration peg formation, the subsequent disease development, and finally sporulation (reviewed in Liu et al. 2011). We observed a periodic development of the disease beginning at 24 h after inoculation and progressing up to 7 d after inoculation (Figure 2). Karki and Sharp (1986) also noted that disease development started from the appearance of small water soaked areas on the leaves 24 h after inoculation followed by the development of visible necrotic lesions 3-4 d later. Keon and Hargreaves (1983) noted that the susceptible host cells started dying near or adjacent to the intracellular hyphae 2 d after inoculation (Figure 2). A chlorotic area starts to develop around the initial necrotic lesion and is thought to be due to the secretion of diffusible toxins or effectors that induce PCD similar to other necrotrophic systems involving closely related fungi (Manning et al. 2009; Liu et al. 2011; Oliver et al. 2010; Oliver et al. 2012).

Karki and Sharp (1986) noted different lesion characteristics in specific barley genotype-isolate combinations, where in general, Montana isolates induced more chlorotic and necrotic type lesions in several barley genotypes compared to Mediterranean isolates. In our study, we also found different lesion characteristics in specific barley accession-isolate combinations (Figure 3). It is likely that specific isolates have different virulence factors that interact with corresponding host factors that confer a distinct visible symptom. Distinctly different visible symptoms have also been shown in the tan spot of wheat pathosystem caused by the closely
related pathogen, *P. tritici-repentis*. In the tan spot of wheat interaction, depending on the host selective toxin (HST) – host gene combination, infection results in necrotic or chlorotic spots, spreading chlorosis, or a combination of necrosis and chlorosis (Reviewed in Faris et al. 2013). These different symptoms have been traced back to three HSTs including *Ptr ToxA*, *Ptr ToxB*, and *Ptr ToxC* and the corresponding host sensitivity genes, *Tsn1*, *Tsc2* and *Tsc1*, respectively (Effertz et al. 2002; Friesen and Faris; 2004; Faris et al. 2010; reviewed in Faris et al. 2013). The different symptoms present in the SFNB pathosystem also indicates the involvement of different pathogen-host combinations that result in different visible phenotypes resulting from a complex system of host-pathogen interactions.

Tekauz (1985) proposed a SFNB rating scale that included ratings of 1-9, with 1-3 being resistant, 5 being intermediate, and 7-9 being susceptible; however, in this scale no 4 or 6 ratings were described, making statistical analysis problematic. Karki and Sharp (1986) proposed a 1-10 rating scale that was based on a combination of lesion size and leaf tip necrosis, that we rarely observed. Therefore, we have proposed a SFNB disease rating scale (Figure 1) that is based on the 1-5 disease rating scale proposed by Lamari et al. (1989) for use with *Pyrenophora tritici-repentis* causal agent of tan spot of wheat, where 1 is most resistant and 5 is most susceptible. Our proposed SFNB scale takes into consideration primarily lesion size but also percent leaf area coverage in the higher reaction types.
Based on reports in the literature of proteinaceous and non-proteinaceous toxins being present in the SFNB and NFNB system (Reviewed in Liu et al. 2011), it is likely that underlying this quantitative trait, there are several effector-host gene interactions that, in combination with one another, result in the different visual phenotypes and varying disease reaction scores. Several of the Pleosporales pathogens in the Dothideomycete class of fungi have been shown to produce necrotrophic effectors that interact with dominant host susceptibility gene products (Reviewed in Wolpert et al. 2002 and Stergiopoulos et al. 2013). The work presented here lays the groundwork for evaluating the genetics of this host-pathogen interaction. Based on this work and the work presented in the adjoining paper, we have provided information about specific accessions and pathogen isolates that are currently being used in host and pathogen population development. The genetic characterization of both virulence and resistance is critical to a complete understanding of this system.

**Diversity in pathogen virulence**

The isolates used in this study were collected from four different barley-growing regions and were therefore expected to have some genetic diversity. Several of the barley accessions evaluated showed a differential reaction between the isolates tested, indicating that each isolate used contained a different set of virulence factors. Interestingly, the FGO isolate collected in North Dakota, where epidemics have recently occurred, harbored the most virulence, with only a few accessions showing lower levels of susceptibility to FGO than the other three. The epidemic in North Dakota has been fairly recent and may be a result of a virulence shift where the local *P. teres f. maculata* population has adapted to current local barley cultivars. Previous studies have also reported a higher virulence of isolates collected in the Northern Great Plains of the United
States and the Canadian prairie region compared to other regions (Karki and Sharp, 1986; Tekauz et al. 1990; Tekauz et al. 1997). SFNB epidemics have also recently been reported in Australia (McLean et al. 2009; McLean et al. 2010) and we found that the average virulence of the Australian isolate SG1 was somewhat lower than the US isolate but higher than isolates collected in New Zealand and Denmark (Table 2-7). Based on our results collected for these four isolates across the 2062 barley accessions, it is likely that the four isolates harbor several common virulence factors; however, each isolate also harbors at least one unique factor with the FGO isolate harboring the most unique virulence factors followed by the Australian isolate SG1. It is likely that the local barley cultivars are driving adaptation in each local pathogen population, however; additional isolates from each of these regions will need to be tested to identify which virulence are unique to each region.
Table 2. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates FGO and SG1.

<table>
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<tr>
<th>Barley Accession</th>
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<th>SG1</th>
</tr>
</thead>
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<tr>
<td>CIho 3694</td>
<td>Egypt</td>
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<tr>
<td>PI 138711</td>
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<td>CIho 14882</td>
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<td>PI 533205</td>
<td>Pakistan</td>
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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the North Dakota isolate (FGO) and the Australian isolate (SG1) are given for each barley accession.*
Table 3. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates FGO and DEN 2.6.

<table>
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<th>Barley Accession</th>
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<th>DEN 2.6</th>
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Table 3. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates FGO and DEN 2.6 (continued).

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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the North Dakota isolate (FGO) and the Denmark isolate (DEN 2.6) are given for each barley accession.*
Table 4. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates FGO and NZKF2.

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Table 4. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates FGO and NZKF2 (continued).

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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the North Dakota isolate (FGO) and the New Zealand isolate (NZKF2) are given for each barley accession.*
Table 5. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates SG1 and DEN 2.6.

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<th>DEN 2.6</th>
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<td>1.3</td>
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Table 5. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates SG1 and DEN 2.6 (continued).

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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the Australian isolate (SG1) and the Denmark isolate (DEN 2.6) are given for each barley accession.*
Table 6. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates SG1 and NZKF2.

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Table 6. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates SG1 and NZKF2 (continued).

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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the Australian isolate (SG1) and New Zealand isolate (NZKF2) isolate are given for each barley accession.*
Table 7. Barley core collection accessions showing a differential reaction between *P. teres* f. *maculata* isolates DEN 2.6 and NZKF2.

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*Underlined numbers indicate higher differential virulence for that isolate. Difference of greater than or equal to 1.8 was set for choosing differential accessions. Country of origin and average disease reactions for the Denmark isolate (DEN 2.6) and the New Zealand isolate (NZKF2) are given for each barley accession.

**Nature of disease resistance**

Tekauz *et al.* (1990) evaluated 42 isolates of *P. teres* f. *maculata* collected in western Canada and showed that 20 different pathotypes were present based on the use of a 12 barley genotype differential set. Similarly, Karki and Sharp (1986) characterized a set of 14 *P. teres* f. *maculata* isolates collected in Montana, USA, Morocco, Tunisia, and Turkey on 20 barley genotypes with 12 of these showing a differential reaction between the isolates tested. These previous studies indicated that virulence variability was prevalent in the populations tested. Based on a gene-for-gene (Flor, 1956) or inverse gene-for-gene hypothesis (Friesen and Faris, 2010), for each pathogen virulence there should be a distinct corresponding host resistance/susceptibility gene and therefore we expected that the BCC tested here should have a high level of resistance diversity. To our knowledge, the study we are presenting here is the first documentation of the screening of a large world barley collection using a diverse collection of *P. teres* f. *maculata* isolates. Based on the diversity of the 2062 barley accessions tested in this study, we would expect that the vast majority of the resistance/susceptibility loci present in
cultivated barley are represented here. It was interesting to note that only a very small percentage of the accessions evaluated showed high levels of resistance to all four isolates tested (Table 2, Figure 5, and Figure 4). Similarly, only a few accessions showed a high level of susceptibility to all isolates tested (Figure 4) with the remainder of the accessions falling in the moderately resistant to moderately susceptible region, resulting in a bell shaped curve. Several accessions showed a strong differential reaction between isolates (Table 2-7) indicating that these accessions harbor resistance/susceptibility that is unique to a specific isolate. The observation of several sources of resistance being effective to only one, two or three but not all of the isolates used in this study along with the normal distribution of reaction types and the fact that several recent outbreaks of this disease have occurred around the world (Liu et al. 2011) are all indications of a complex host pathogen interaction that is highly variable in the natural population. This makes the complete characterization of both host resistance and pathogen virulence critical. The disease reaction information presented here lays the foundation for further studies involving the characterization of these resistance sources. Currently, barley populations are being developed using resistant accessions identified here and resistance/susceptibility loci have been mapped by an association mapping strategy utilizing the phenotyping data generated in this study (Tamang et al. 2014, unpublished). The overall goal is to characterize the different sources of broad resistance and intelligently deploy them in regional barley cultivars.
Figure 5. Uniformly resistant barley lines seven days post inoculation using *P. teres* f. *maculata* isolates FGO, SG1, NZKF2 and DEN 2.6. Barley accessions used were the five most resistant accessions: PI 61584 (A), PI 296996 (B), PI 640382 (C), PI 84314 (D), and PI 67381 (E) for each isolate inoculation.
Based on this study we can conclude that resistance to P. teres f. maculata is complex. This complexity is likely due to the number of distinct virulence loci in the pathogen and the distinct corresponding resistance/susceptibility loci present in the host. The isolates used in this study have been used to develop mapping populations to evaluate the genetics of virulence and the resistant barley accessions are being used in population development for the characterization of resistance/susceptibility, leading to a better understanding of this important host pathogen interaction.

Literature Cited


Tekauz, A., and Buchannon, K. W. 1977. Distribution of and sources of resistance to biotypes of 


Williams, K. J., Lichon, A., Gianquitto, P., Kretschmer, J. M., Karakousis, A., Manning, S., 
99:323–327.

2003. A comparison of the genetics of seedling and adult plant resistance to the spot form of net 

APPENDIX. ALL BARLEY ACCESSIONS USED AND THEIR AVERAGE DISEASE REACTION USING EACH ISOLATE

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