Fungal Genetics and Biology 79 (2015) 3–7

Contents lists available at ScienceDirect

Fungal Genetics and Biology

journal homepage: www.elsevier.com/locate/yfgbi

The impact of Septoria tritici Blotch disease on wheat: An EU perspective

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ARTICLE INFO

Article history:
Received 22 January 2015
Revised 30 March 2015
Accepted 1 April 2015

Keywords:
Septoria tritici Blotch
Wheat
Crop yields
Economic value

ABSTRACT

Zymoseptoria tritici is the causal agent of one of the European Union's most devastating foliar diseases of wheat: Septoria tritici Blotch (STB). It is also a notable pathogen of wheat grown in temperate climates throughout the world. In this commentary, we highlight the importance of STB on wheat in the EU. To better understand STB, it is necessary to consider the host crop, the fungal pathogen and their shared environment. Here, we consider the fungus *per se* and its interaction with its host and then focus on a more agricultural overview of the impact STB on wheat. We consider the climatic and weather factors which influence its spread and severity, allude to the agricultural practices which may mitigate or enhance its impact on crop yields, and evaluate the economic importance of wheat as a food and animal feed crop in the UK and EU. Finally, we estimate the cost of STB disease to EU agriculture.

1. Introduction

Septoria tritici Blotch (STB) poses a serious and persistent challenge to wheat grown in temperate climates throughout the world. This threat has triggered an intensive research effort to evaluate current disease control practices and to look for novel control strategies. Despite the huge economic importance of this pathogen (contained within this article and in Torriani et al., 2015), solid facts in peer-reviewed publications regarding yield losses or, indeed, the financial implications of disease are hard to find. For example, published losses due to STB disease recorded in one particular study in a defined geographic region have become widely adopted in the literature as being relevant to losses in all regions of the world (Eyal et al., 1973, 1987). Such extrapolations should not form the basis for economic, political and agricultural decision-making. In this article, we therefore set out to collate all available information, gathered from peer-reviewed scientific publications, publically accessible data-bases and web-sites, to paint a more realistic picture of the importance of STB in Europe. We hope that this merged information provides a solid basis with which we can evaluate the challenge of STB disease in Europe.

2. The importance of wheat as an EU crop

Wheat is the most widely-grown crop in the world. Global harvests reached 705 million metric tonnes (mmt) in 2013–2014 (www.agrimoney.com/). Within the EU, wheat advances from its world position of second most important food crop (after rice) to the status of most important cereal. In 2013/2014 the various countries which comprise the EU produced over 143 mmt of wheat; some 15% more than China, 35% more than India and 60% more than USA (calculations based on www.fao.org/worldfoodsituation/en/). Of the various EU member states, France and Germany are the biggest wheat producers, harvesting circa 26% and 17% respectively of the EU total, with UK gathering around 8.5% (Table 1). Over the past 10 years, EU metric tonnage has increased by 23%, whilst, over the same period, US tonnages have fallen by around 8% (faostat3.fao.org/).

The EU currently exports up to 15% of its harvest (ec.europa.eu/agriculture/cereals) and this figure is rising annually. Wheat grain grown in the EU provides calories for human foodstuffs (less than one third of harvest) and animal feed (circa two thirds of harvest). Wheat is also grown for alcohol distillation, as a raw material for biofuels and wheat straw is used for livestock bedding and fodder, roof thatching and basket-making.

Such figures and statistics attest to the huge economic and social importance of wheat as an EU crop and commodity. It follows that losses to the wheat crop from attack by pests and infection by pathogens are of considerable concern. Of the various pathogens, the foliar disease of wheat, Septoria tritici Blotch (STB), caused by the fungus *Zymoseptoria tritici*, is most problematic in our wheat fields (Shaw and Royle, 1989; Eyal et al., 1987). *Z. tritici* flourishes in the humid climate that prevails in EPPO's "Maritime Zone" (Bouma, 2005 EPPO bulletin 35). This climatic region includes Northern France and Germany, as well as the UK. Thus, the fungus pervades the major wheat growing regions of

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http://dx.doi.org/10.1016/j.fgb.2015.04.004
1087-1845/

Table 1
Wheat harvests and value in the 3 main EU wheat growing nations.

WHEAT – (2013 harvest)	France	Germany	UK
Hectares planted (million)	4.95	3.1	1.63
Yield: tonnes per hectare	7.4	8	7.4
Harvest total (m Tonnes)	37	24.9	12.1
Value per tonne (Euros)	195	195	195
Value to economy of named country (million Euros)	7200	4900	2400

Data from: Analyst Agritel; Agri.eu/wheat-market; Farming-statistics@defra; Federal ministry of food and agriculture; International grain council wheat index; Agrimoney.

the EU. In fact, this persistent pathogen accounts for approximately 70% of annual fungicide usage in the EU. During severe epidemics, losses of up to 50% of yield have been documented in fields planted with wheat cultivars susceptible to STB (Eyal et al., 1973: Eyal et al., 1987). In the UK, annual losses averaging around 20% of harvest are recorded when susceptible varieties on the 2012–2013 Home Grown Cereal Authority (HGCA) recommended list are deployed (www.hgca.com/media/.../ts113_septoria_tritici_in_winter_wheat.pdf) and are not treated with fungicides. However, smaller yield losses, of around 5–10%, are seen when wheat varieties are selected for disease resistance and when crops are sprayed with fungicide (hgca.com/.../g58-wheat-disease-management-guide-feb-2014). For the 25 wheat varieties recommended for autumn planting (winter wheat) HGCA give an average resistance score of 5 on a 1–9 scale in which high numbers indicate high resistance (HGCA recommended list^{R}). Although this resistance is only partial, and thus some yield losses are still incurred, it has proven durable – advantageously – against all known fungal genotypes (Angus and Fenwick, 2008; Chartrain et al., 2015).

3. *Zymoseptoria tritici* as a threat to wheat production

The fungus, *Z. tritici*, has remained a relatively understudied pathogen (reviewed in: Kema et al., 1996; Duncan and Howard, 2000; Palmer and Skinner, 2002; Orton et al., 2011; Steinberg, 2015), particularly with regards to the paucity of molecular and cellular-based tools to interrogate the fungus *per se* (addressed in this issue). Moreover, our restricted knowledge of the interaction between the fungus and its host constrains our ability to optimise STB disease control strategies. For instance, this dimorphic pathogen exhibits an unusual and protracted 'latent' phase following its arrival on wheat (rev. in Orton et al., 2011). This phase describes a period when the fungus is associated with the leaf, but where the leaf exhibits no disease symptoms. Under field conditions in the summer this period persists for around 14 days, with this time protracted in colder weather up to 28 days (HGCA data). Whilst some very low level fungal activity has been described during this latent period (Keon et al., 2007; Shetty et al., 2007), a full understanding of its nutrient acquisition strategy and of its fine-scale temporal and spatial interactions with wheat remains elusive (Rudd et al., 2015; Sánchez-Vallet et al., 2015). Our state of knowledge regarding the molecular cross-talk between *Z. tritici* and the wheat immune system is elegantly summarised in O'Driscoll et al. (2014). Indeed, the timing of fungicide application is somewhat problematic, as it is difficult to match it confidently with disease progression. Fungicides sprayed at disease onset are effective for approximately seven of the 14–28 day latent period. Thus, whilst the leaves remain asymptomatic and the farmer considers that disease has been eradicated, it is possible that in fact the fungus proliferates. Best practise therefore requires that fungicide be sprayed early, before disease appears, to protect developing stem leaves, and again at ear emergence, to protect the flag and upper leaves (http://www.hgca.com/media176167/g63-wheat-disease-management-guide.pdf). However, if lesions begin to show on the leaves, STB has taken hold and fungicide application will be of limited utility. Few curative fungicides – chemistries that prevent pathogen colonisation of host tissues – are available. Those fungicides which are curative towards STB are among those to which resistance is developing (in particular, the azoles).

Z. tritici shows many characteristics typical of fungal plant pathogens – it has, for example, a mixed reproductive system and can generate large populations of spores (see below). Substantial gene flow can occur between fungal strains (Zhan and McDonald, 2004), with up to 30% of the *Z. tritici* population at the end of a growing season resulting from sexual reproduction (Eriksen et al., 2001) – a trait likely to decrease the time needed for it to adapt to control measures. Moreover, genome sequencing has revealed some unusual "hallmarks" in *Z. tritici* (Goodwin et al., 2011: Stukenbrock et al., 2010). The fungus carries 21 chromosomes, with thirteen core and eight dispensable chromosomes (meaning that they are supernumerary or accessory and can be lost without obvious effects on fungal fitness; commentary in Croll and McDonald, 2012). Around 17% of the genome is estimated to be repetitive. Of this, 70% is enriched in class 1 transposable elements (retro-elements which amplify *via* an RNA intermediate, thus introducing new mutations). The dispensable chromosomes carry a higher percentage of repetitive elements than the core chromosomes (Dhillon et al., 2014). Further, genes on these dispensable chromosomes which have homologues in the core chromosomes of sister species show an accelerated rate of evolution compared with these core genome homologues (Stukenbrock et al., 2011). The ability to dispense with up to eight chromosomes suggests, *a priori*, that this could hasten the loss of core fungicide target genes, that the fungus may develop resistance to fungicides (Torriani et al., 2009; Cools and Fraaije, 2013), alter its host-specificity (Stukenbrock et al., 2010) or, indeed, become able to overcome host disease resistance (Mundt et al., 1999, 2002; Rudd et al., 2015). Although these ideas are, at present, speculative, such suggestions merit investigation.

Modern agricultural practices have favoured the planting of vast hectarages of genetically uniform crops. Wheat fields in Europe are extensive and are planted with just a handful of cultivars moderately resistant to STB. Such practice favours the build-up of inoculum levels, so potentially hastening the emergence of new fungal pathotypes both from sexual reproduction between compatible strains (or indeed incompatible strains, see Kema et al., 2000) and via emergence of aggressive strains from a vast population of asexual spores. But how large are these fungal populations and what is the risk of new strains emerging? We can, for example, estimate the STB asexual spore load per hectare in a growing season. Planting densities for wheat are around 100 plants per m^2, with each plant carrying 5 leaves. There are therefore up to 5×10^6 wheat leaves receptive to inoculum per hectare. Assuming the asexual pycnidiospore generation to generation time is around 20 days, then, over a growing season, this polycyclic pathogen can cycle up to 6 times on a maturing crop. If the average disease rating for the wheat cultivars is 5 (HGCA listing) and infected wheat with this level of partial resistance generates 20 lesions per leaf (Jenna Watts, HGCA *pers. com.*) each 10 mm^2, with 2 pycnidia per mm^2 (see Fones et al., this issue), then a leaf could carry 400 pycnidia. Mature pycnidia fill the wheat substomatal cavity and carry approximately 300 spores (Fig. 1). Not all pycnidiospores would mature simultaneously nor be competent to infect but, from this, we can estimate that the asexual spore load per hectare over a growing season may reach 10^{10-11} spores. Whilst not all rain-splashed spores will cause infection, this high pathogen load, coupled with the "plasticity" of the *Z. tritici* genome, means that emergence of new fungal strains is of grave concern.