Temporal and spatial field evaluations highlight the importance of the pre-symptomatic phase in supporting strong partial resistance in *Triticum aestivum* against *Zymoseptoria tritici*

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Abstract

Zymoseptoria tritici, the causal agent of septoria tritici blotch (STB), remains a significant threat to European wheat production with the continuous emergence of fungicide resistance in *Z. tritici* strains eroding the economic sustainability of wheat production systems. The life cycle of *Z. tritici* is characterised by a pre-symptomatic phase (latent period, LP) after which

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the pathogen switches to an aggressive necrotrophic stage, when lesions bearing pycnidia quickly manifest on the leaf. As minimal knowledge on the possible role of the LP in supporting STB resistance/susceptibility exists, the goal of this study was to investigate the spatial and temporal association between the LP and disease progression across 3 locations (Ireland – Waterford, Carlow; UK – Norwich) that represent commercially high, medium and low STB pressure environments. Completed over two seasons (2013-2015) with commercially grown cultivars, the potential of the LP in stalling STB epidemics was significant as identified with cv. Stigg, whose high level of partial resistance was characterised by a lengthened LP (~36 days) under the high disease pressure environment of Waterford. However, once the LP concluded it was followed by a rate of disease progression in cv. Stigg that was comparable to that observed in the more susceptible commercial varieties. Complementary analysis via logistic modelling of intensive disease assessments made at Carlow and Waterford in 2015, further highlighted the value of a lengthened LP in supporting strong partial resistance against STB disease of wheat.

1. Introduction

Zymoseptoria tritici, the causal agent of septoria tritici blotch (STB), is a serious and persistent threat to global wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) production, causing yield losses of up to 50% where susceptible wheat varieties are grown under weather conditions conducive to STB development (Eyal et al., 1987, Fones & Gurr, 2015). In the absence of commercial varieties with durable resistance, the cereal sector is currently reliant on extensive fungicide programmes to mitigate against the disease. As a result over 70% of annual EU fungicide usage in wheat is targeted towards STB (Fones & Gurr, 2015), supporting a fungicide market worth ~ €1.2bn per annum (Torriani et al., 2015).

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Owing to a humid, temperate climate, fungicide programmes are an indispensable component of North-western European grain production systems, with yield response to fungicide use conveying the potential for strong financial returns (Lynch et al., 2017). However, such chemical over-dependency has driven the evolution of fungicide insensitive/resistant phenotypes of *Z. tritici*, which to date has negated the efficacy of the methyl benzimidazolecarbamates (MBCs) (Griffin & Fisher, 1985), the quinone outside inhibitors (QoIs) (commonly referred to as the strobilurins) (Fraaije et al., 2005) and continues to reduce the effectiveness of the demethylase inhibitors (DMIs) (Stammler & Semar, 2011). While the efficacy of the succinate dehydrogenase inhibitor (SDHI)-based fungicides remains for the moment, the emergence of the H152R mutation in isolates of *Z. tritici* collected from commercial wheat crops (Dooley et al., 2016a) reflects the ever-increasing threat of continued extensive fungicide use to sustaining current wheat production. Current advice recommends mixing active ingredients with alternative modes of action (Torriani et al., 2015) to slow the emergence of fungicide resistance among field populations (Dooley et al., 2016b), but it does not necessarily follow that it will equally preserve each chemistry in the mixture (Dooley et al., 2016c). The issue is further compounded within Europe by the reversal of protection-product registrations from a risk-based to a hazard-based assessment, as per Regulation No 1107/2009. Such legislative constraints have already resulted in a loss of approximately 20% of active ingredients used for STB control (Grimmer et al., 2015) and will likely lead to the prohibition of most DMI-based fungicides (Jess et al., 2014). Taken together the wheat production sector, in North Western Europe especially, is facing an unsustainable future unless greater emphasis is placed on developing durable genetic resistance to STB.

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The narrow genetic diversity of common hexaploid wheat is as a consequence of a limited number of individuals involved in the evolution of wheat (Feuillet et al., 2008, Reif et al., 2005, Li et al., 2014). While this complicates the identification of novel sources of genetic resistance to STB within the current gene pool, an association genetics (AG) analysis has shown that combining genes associated with quantitative resistance in well-adapted germplasm can assist in breeding durable resistance through transgressive segregation (Arraiano & Brown, 2016). Alternatively, looking outside the current gene pool of cultivated wheat lines, synthetic hexaploids may also present a rich source of genetic resistance to STB (Brown et al., 2015). Indeed, synthetic hexaploids have proven to be a novel source of qualitative resistance against STB with several genes identified to date (Brown et al., 2015), with Stb16q (from the diploid wild wheat species *Aegilops tauschii*) of particular interest to breeders as it, so far, confers broad-spectrum resistance at the seedling stage to all *Z. tritici* isolates tested (Ghaffary et al., 2012).

Accepting that high quantitative resistance can maintain/increase durability as it will persist at a higher frequency than a genotype with qualitative resistance (Brown, 2015). Therefore, it would appear logical that any extension in the pre-symptomatic phase of the *Z. tritici* disease cycle would represent an important step in supporting a more durably resistant phenotype due to the overall reduction in airborne pycnidiospores within the crop canopy. Yet, the molecular and environmental triggers responsible for the pre-symptomatic phase of the *Z. tritici* life cycle, referred to as the latent period, remain unclear (Steinberg, 2015, O'Driscoll et al., 2014) to the point that the classification of *Z. tritici* as a hemibiotroph still remains questionable (Sánchez-Vallet et al., 2015).

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The duration of the latent period is dependent on multiple factors including, but not limited to, wheat genotype, varietal growth stage when inoculated, environmental conditions and inoculum density (Hess & Shaner, 1987, Thomas et al., 1989, Shaw, 1990, Armour et al., 2004, Lovell et al., 2004, Viljanen-Rollinson et al., 2005, Henze et al., 2007). Not surprisingly, based on the epidemiology of *Z. tritici* in the field, varieties that induce longer latent periods tend to slow down disease progression (Viljanen-Rollinson et al., 2005). However, previous reports on the relationship between LP and variety performance are predominantly based on controlled-environment experiments or field experiments where STB inoculum is artificially applied (Lovell et al., 2004, Armour et al., 2004, Viljanen-Rollinson et al., 2005, ŠÍP et al., 2015). While informative, this experimentation can be limited due to the restricted number of isolates employed and hence may not provide scope to determine the durability of the studied genotypes.

The primary goal of this study was to examine the spatial and temporal influence of natural disease pressure on the interaction between latent period (referred to in this paper as the time of flag leaf emergence to the first appearance of lesions bearing pycnidia) and disease progression within a collection of commercial varieties. Completed across three geographic locations that qualitatively represent high, medium and low levels of STB pressure, this study identified the genetic potential of the synthetically derived *T. aestivum* cv. Stigg to impede STB epidemics in a commercial setting. In the context of the studies presented here, cv. Stigg maintained its strong partially resistant phenotype due to a significant increase in the duration of the latent period on its flag leaf. However, once this period was concluded cv. Stigg exhibited a rate of disease progression comparable to that observed in susceptible genotypes.

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2. Materials and Methods

2.1 Studies performed

A glasshouse study was undertaken as a preliminary assessment of variety specific latent periods under controlled conditions, prior to completing the larger field study. Seeds of seven winter wheat varieties (Table S1) were pre-germinated in the dark at 20ºC on moist Whatman No.1 filter paper (Whatman International Ltd., England) for 3 days to synchronise germination. Germinating seeds were placed in 8 x 8 x 8 cm pots (5 plants per pot) with John Innes number 2 compost (Bord Na Mona, Ireland), in a controlled glasshouse, under a 12 h day/night cycle at 18/12ºC, respectively. After 2 weeks growth (GS 12; (Zadoks et al., 1974) the 2nd leaf was treated until run-off with a *Z. tritici* pycnidiospore suspension (isolate IPO323; spore concentration 1 x 10^6 ml^{-1}) and 0.2 % Tween 20 using a hand-held sprayer. Controls were treated with water and 0.2 % Tween 20. Pots were covered with clear polythene bags for 96 hours to maintain humidity. The study included 3 pots per treatment with two independent experiments completed. Latent period was calculated as days from inoculation to first appearance of lesions bearing pycnidia.

The field study was completed through the 2013-2014 and 2014-2015 seasons across three locations (Carlow and Waterford in Ireland and Norwich in the UK), which provided contrasting STB pressures as per previous studies (data not shown). Varietal selection is detailed in Table S1 and all crops were established, treated and harvested according to conventional practise, with the exception that there was no fungicide applied to control *Z. tritici.* In both seasons, plot sizes were 1.5 x 3m in Waterford, 2.5 x 6m in Carlow and 1.5 x 6m in Norwich with five-fold replication across a replicated randomised block design. In both studies powdery mildew and leaf rust control was achieved with a mixture of Amistar (half rate 0.5l/ha; Syngenta) and Corbel at (half rate 0.5 l/ha; Bayer Crop Science, Ireland) (Table

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1). As the G143A mutation continues to dominate the Irish and UK *Z. tritici* population, applications of Amistar had no negative impact on STB incidence and progression. For the Irish sites weeds were controlled by post-emergence herbicides Ally Max (metsulfuron methyl and tribenuron methyl, DuPont, United Kingdom) at 0.5 l/ha plus (4-chloro-2-methylphenoxy) propanoic acid (CMPP, Syngenta, Ireland) at 0.75 l/ha. Growth regulators chlormequate chloride (CCC, BASF Crop Protection, Ireland) and Terpal (mepiquat chloride, BASF Crop Protection, Ireland) were applied at 1.0 l/ha. At the Norwich site, Defy (prosulfocarb, Syngenta UK) and Hurricane (diflufenican, Adama) was applied pre-emergent at 4.0l/ha. Atlantis (mesosulfuron-methyl and iodosulfuron-methyl-sodium, Bayer) was applied at approximately GS 25 at 0.4kg/ha, with Ally Max (tribenuron-methyl and metsulfuron-methyl, Du Pont) applied at GS31/32 at 42g/ha and Starane (fluroxypyr, DowAgro) applied at GS39 at 1.0l/ha. In addition, plant growth regulators (chlormequat chloride; 3C Cycoce, BASF Crop Protection UK and Terpal, Mepiquat Chloride and 2-chloroethylphosphonic acid, BASF Crop Protection UK) were applied at 1.0l/ha. As it was a challenge to control yellow leaf rust on susceptible varieties in Norwich in the 2013-2014 season, it was not possible to collect data for Gator and Kielder for that site x year.

2.2 Disease assessments

STB severity on the flag leaf of field grown plants was assessed on 10 tagged tillers/plot with STB assessments conducted twice weekly through to senescence. Disease severity was recorded as the percentage flag leaf with lesions bearing pycnidia (PFLP). Approximate flag leaf emergence dates were recorded for Carlow and Waterford (2015) sites (Norwich data was unavailable) for each variety with the subsequent time (i.e. latent period) to the first appearance of disease area bearing pycnidia on 50% of tagged leaves also recorded.

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2.3 Profiling the rate of STB progression

To estimate the rate of disease progression (RDP; slope at 5-80% PFLP) for each variety, logistic curves were fitted to the PFLP data derived from each variety assessed at Carlow and Waterford (excluding Gallant) in 2015 (due to availability of flag leaf emergence data) using the equation:

$$y = a + \frac{c}{(1 + e^{(-b \times (x-m))})}$$

Estimations of disease progression were calculated for multiple regression models with a logistic model chosen as the accuracy of fit was deemed significant at $P<0.05$. To determine the slope value that corresponds to specific PFLP scores the equation used was:

$$\text{Rate of disease progression} = \frac{b \times c \times e^{(\ln\,(\frac{c}{y-a}-1))}}{(1+ e^{(\ln\,(\frac{c}{y-a}-1))})^2}.$$

To determine the degree day (^{o}days) value that corresponds to specific PFLP scores the equation used was:

$$\text{degree days (x)} = \frac{\ln\,(\frac{c}{y-a} - 1)}{-b} + m$$

In all equations, y= STB severity, x= thermal time (^{o}Days value) and a, b, c and m, are parameters determined by the statistical fitting of the logistic curve within GeneStat (14th edition; VSN International Ltd., Hemel Hempstead, UK; 2011). In this model, parameter 'a' impacts the average PFLP on the initial phase of the logistic curve, 'b' impacts the rate of increase of PFLP during the intermediate phase, 'c' impacts the PFLP at the final phase and 'm' impacts on the thermal time at the end of the intermediate phase. ^{o}Days were calculated using a base temperature of 0°C at flag leaf emergence and accumulated from flag leaf emergence to senescence. Prior to completing the logistic analysis on the plot means, logistic curves were first calculated for each replicate plot per variety to determine non-significance and conformity to the variety-specific curves being generated.

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2.4. Data analysis

Basic data analysis was performed using Microsoft Excel 2010 with statistical analysis of the data completed using Minitab (Minitab Release 13.32©, 2000, Minitab Inc.) or GenStat (14th edition; VSN International Ltd., Hemel Hempstead, UK; 2011). Data from the glasshouse study was analysed as per Analysis of Variance (ANOVA). For the field study, the impact of variety, location and year on recorded STB PFLP was determined using ANOVA, with comparisons between means of each variety performed using a Fisher's protected LSD test within Genstat. The relationship between the variety-specific latent period and PFLP over time (calculated as the area under the disease progress curve (AUDPC) for the flag leaf) was examined on 2015 data recorded from Carlow and Waterford.

To examine the profile of disease progression, logistic curves were fitted using the standard curve procedure in Genstat and the significance of the rate of STB disease progression determined via one-way ANOVA of the slope of the line taken at multiple PFLP values (5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75 and 80%) of the respective fitted logistic curve. For comparisons, Fisher's protected LSD test within Genstat was employed. Separately, the significance/non-significance of degree days at multiple PFLP values across varieties was calculated, with Fisher's protected test also used to calculate the least significant difference between varieties. Logistic curve fitting was first completed on the mean disease scores/accumulated degree days of each replicate plot (with 10 tagged leaves / plot) per variety to ensure non-significance within replicates before completing the assessment on mean variety values.

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3. Results

3.1 Controlled climate evaluation of the latent period of individual variety-*Z. tritici* interactions

Latent period (LP) varied from 22.1 days (cv. Kielder) to 34.8 days (cv. Stigg). The LP of the Stigg – *Z. tritici* interaction was significantly ($P<0.05$) longer compared to the other varieties studied, with cv. Stigg being the only variety tested with an LP > 30 days post inoculation (Figure 1). Outside of these min and max values (for Kielder and Stigg respectively), varieties Gator and Oakley had approximate LPs of approximately 25 days, while Dunmore, JB Diego and Croft had LPs of 28 to 29 days.

3.2 Assessing field-based development of STB on *T. aestivum* varieties that support divergent latent periods

Across the first season (2013-2014) higher levels of STB disease pressure were recorded in Waterford (Table S4) compared to Carlow (Table S3), which in turn was higher than Norwich (Table S5). This pattern was repeated in the second season (2014-2015) (Table S6, S7, S8); as supported by the climatic conditions at all three locations for both seasons (Table S2). Examining disease progression in more detail, similar varietal rankings (at 50% PFLP, high-to-low susceptibility) were observed across the sites for the 2013-2014 season: Waterford - Gator, Kielder, Croft, Dunmore, JB Diego, Stigg; Carlow – Gator, Kielder, Dunmore, Croft, JB Diego, Stigg; Norwich – Croft, Dunmore, JB Diego, Stigg (Figure 2). For the 2014-2015 season, variety rankings from Waterford and Carlow (at 50% PFLP) were Gallant (most susceptible) followed by an alternating group of Gator, Croft, Kielder, Dunmore, JB Diego after which Stigg recorded the lowest disease level at both sites, which was also recorded at Norwich (Figure 3). However, for Norwich the order of the varieties was Gator (most susceptible), JB Diego, Croft, Gallant, Kielder, Dunmore and Stigg; at only 10%

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PFLP, due to the low incidence of STB disease that summer, possibly due to higher mean temperatures and lower mean monthly rainfall (Table S2). Overall, Stigg recorded consistently lower levels of disease across all three assessment sites and two growing seasons (P>0.001, Figure 2-3), which was evident by the corresponding delay in disease progression as represented by ^{o}day (Table S3 – S8). This was supported by the association of variety AUDPC values and the time to first appearance of lesions bearing pycnidia relative to flag leaf emergence (Figure 4, Carlow and Waterford, 2015 only). With the exception of Stigg, studied varieties grouped according to location, with higher AUDPC values recorded from Waterford as opposed to the same varieties in Carlow. Of interest, the reduction in days (latency period) for cv. Dunmore and JB Diego from Carlow to Waterford was not reflected in a corresponding increase in AUDPC, in contrast to the more susceptible varieties of Gallant, Gator, and Kielder (Figure 4).

3.4 Modelling STB progression

As flag leaf emergence dates were recorded at Waterford and Carlow in 2015, it was possible to apply a logistic model to examine in more detail STB disease progression (Figure 5) by comparing slope values (Table 2, 3) for each disease progress curve relative to the ^{o}day values (Table 4, 5) at set PFLP scores. With the exception of Gator, the slope values returned for each variety's disease progress curve in Waterford (Figure 5a) were similar, with Stigg, JB Diego and Dunmore found to be equivalent from 5% to 20% PFLP (Table 2). From 25% to 40% there was no significant difference between Stigg, Kielder, Dunmore and Croft while from PFLP values of 45% to 65% the rate of disease progress in Stigg and Kielder were also comparable relative to those of JB Diego, Dunmore and Croft (Table 2). In contrast, a clear separation between the varieties is evident from the degree day values through the same PFLP scores from Waterford (Table 4). For example the occurrence of 5% PFLP of the flag

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leaf (1st value where it was possible to model for all 6 varieties) was recorded on Stigg at 783 ^{o}days, an average of 138 ^{o}days (17.6%) later than the occurrence of the same level of disease on the other 5 varieties, with Croft at 609 ^{o}days the first to record 5% disease. As disease progressed in this field study, this differential in the mean varietal ^{o}days (for Croft, Dunmore, Gator, JB Diego, Kielder) versus the corresponding ^{o}days for Stigg was sustained, decreasing to 135 ^{o}days at 20% and 25% PFLP while increasing to 179 ^{o}days at 75% PFLP (Table 4), at which point the slope of the disease progress curve for Stigg was significantly different ($P<0.001$) than the remaining varieties (Table 2).

Modelling STB progression for data taken from the Carlow site (Figure 5b), the slope values for Stigg were significantly higher ($P<0.001$) than those of the other varieties in the study from 5 to 25% PFLP. Thereafter to 55% PFLP, there was no difference between Stigg, Kielder, JB Diego, Gator, Gallant, Croft and to a lesser degree, Dunmore (Table 3). From 60 to 70%, the slope of the curve for Stigg decreased significantly being more in line with Dunmore, with the remaining varieties grouping together. From the perspective of ^{o}days, PFLP on Stigg reached 5% 190 ^{o}days later than the mean ^{o}day value of the remaining varieties. In contrast to Waterford, this value decreased steadily through the season, to 137 ^{o}days by the time 60% of the flag leaf surface contained lesions bearing pycnidia (Table 5).

4. Discussion

The destructive potential of STB has been well-documented (Fones & Gurr, 2015, O'Driscoll et al., 2014, Torriani et al., 2015). Coupled with the substantial concern over the loss of fungicide efficacy and further restrictions on their use, there is now greater urgency for breeding varieties for STB resistance (Jess et al., 2014). The fundamental requirements for accurately identifying durable STB resistant wheat phenotypes are adequate genetic diversity

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within the studied germplasm and field trial sites where consistent STB epidemics occur so effective selection can be conducted (Brown et al., 2015). The locations described here for the field study were selected on the premise that they would bring to the study exposure to graded levels of natural *Z. tritici* inoculum, with the hypothesis that Norwich, Carlow and Waterford would provide low, medium and high levels of STB disease pressure. Based on the levels of STB disease recorded for Carlow along with the disease pressures at Norwich and Waterford relative to Carlow in both seasons, the relative performance of the locations was as predicted, providing a unique element to the study.

Taken together, the data collated from all three sites affirms the finding that environmental conditions at different trial sites, have a significant impact on varietal STB resistance levels (Schilly et al., 2011, Zalewski et al., 2009) and highlights the benefits of deploying quantitative resistance to limit disease pressure within a growing season. As is the nature with field studies, environmental and logistical challenges were observed. Here, the intensive data collection achieved at Carlow in Waterford during the field study, was not possible at Norwich. Meanwhile, there was earlier than predicted crop development through the 2013-2014 season, which in the case of Carlow and Waterford prevented an accurate recording of flag leaf emergence and hence impeded follow on logistic modelling of that year's datasets. Nevertheless, varieties in general (e.g. Stigg; resistance rating 8; Dunmore with a rating of 6 and Gallant with a rating of 3; as per Irish Recommended List (RL) (https://www.agriculture.gov.ie/farmingsectors/crops/cropvarietyevaluationcve/cvepublicationsinformation/) ranked the same across location-seasons, reflecting their national list ratings. Of interest though, JB Diego which has a low RL rating of 5, consistently recorded the second highest resistant phenotype in the field, indicating its resistance score may not be wholly reflective of its phenotype.

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Lynch et al., (2017) recently reported that the use of varieties that exhibit strong STB resistance (such as Stigg), can reduce the economic optimum fungicide dose and the economic risk of sub-optimal STB control. This is significant in light of current legislative drivers requiring reductions in pesticides applied and the corresponding implementation of IPM-based strategies to protect crop outputs. The assessments described here indicated the role of an extended latent period in supporting the Stigg phenotype but it was also observed under field conditions (and complemented with presented modelling) that the rate of disease progression appeared similar to the other varieties upon conclusion of the latent period. Stigg's resistance is therefore largely expressed as a substantial delay in the latent period compared to other, more susceptible varieties.

The varieties used for the field study were chosen based for the most part on the contrasting LPs recorded in the glasshouse study and overall this difference in LPs was also reflected in the field. However, differences were observed between sites in the 2014-2015 season with longer LPs (averaged across all varieties) in Carlow (34.2 days) compared to Waterford (21.9 days), where warmer, early season temperatures and higher rainfall in the summer months facilitated the shorter periods. Notwithstanding the possibility that there was a time lag in flag leaf infection post-emergence in Carlow compared to Waterford, indicating that regional environmental conditions affect the latent period of *Z. tritici* (Eyal, 1987, Armour et al., 2004, Viljanen-Rollinson et al., 2005), this also highlights the necessity to gauge adult plant resistance across multiple field locations so that adequate phenotyping datasets can be generated in support of breeding strategies.

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Significant inter-varietal latent period variation was also noted, with Stigg (36.5 days) recording almost double the LP compared to Gallant (21.3) at both Waterford and Carlow (2014-2015). At 36.5 days, the LP of cv. Stigg is almost equivalent to the lifetime of the flag leaf, which based on the modelling applied in this study implies there is little time remaining for STB disease to develop and disperse through the canopy. As cv. Stigg is able to suppress disease development in this manner, a question for future research needs to focus on how the end of the LP in cv. Stigg relates to the onset of senescence. For example, is the resistance observed an active process of suppressing pathogen growth or development or both, and does that suppression fail once the leaf starts dying for it is clear that Stigg's resistant phenotype decreases rapidly as PFLP progresses, as exhibited in Carlow and Waterford. A further study which measures the expression of natural senescence markers: e.g Senescence Associated Gene (SAG) homologues in wheat (Kajimura et al., 2010), during set stages of PFLP would shed more light on the effects that natural senescence has on loss of resistance in cv. Stigg.

While the association between latent period and AUDPC highlights the value of utilising extended latent periods as a potential mechanism to impede STB epidemics, especially in high disease pressure environments, an obvious question is *how different does the latent period need to be to have a significant ability to impede STB?* The inclusion of the Carlow and Waterford sites in the study provides some insight on this for at Carlow only 4 days separated Stigg, Croft, Dunmore and JB Diego in regards to the observed period (averaging 35 days) before lesions bearing pycnidia first appeared. In contrast, under the high STB pressure evident at the Waterford location the difference between Stigg and the same varieties in Waterford was up to 15 calendar days, with Stigg reporting a 35 day period. While a 35 day period provides confidence to impede STB incidence, the mitigating factor in answering the question remains the location and its propensity for STB incidence. While

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increasing the time between the pathogen's life cycles, has a knock on effect on reducing the spread of inoculum up through the canopy, the data also suggests that as disease pressure increases, as seen in Waterford, there is a greater disparity between resistance phenotypes such as Stigg and susceptible varieties (e.g Gallant), emphasising the necessity of prioritising the selection of resistant germplasm in areas with a high risk of septoria outbreaks. Indeed, if novel varieties with Stigg-related resistance (or similar) are brought to market in the near future, it will be interesting to determine their relative impact at a regional level in regards to the levels of over-wintered inoculum coming off respective fields, versus for example sites that were cultivated with an STB susceptible variety. To achieve this though, there is a need to first identify a suitable proxy for measuring the LP in wheat as a substitute for the time and labour intensive process adopted here. Such a proxy score could simply be a measure of disease present after a specific period post-flag leaf emergence, assuming an accurate recording of the latter. In any event, to be a pragmatic tool for breeders it must be cost-effective and quick to score.

Unfortunately, the molecular mechanism involved in duration length in LP of varieties is not well understood (O'Driscoll et al., 2014) and thus selection of varieties on the basis of LP duration length remains limited to phenotypic screens. A comprehensive study by Rudd et al. (2015) has detailed the genetics supporting the latent period of *Z. tritici*'s interaction with the susceptible variety Riband. This was associated with the downregulation of putative host defence genes including PR proteins, WRKY transcription factors and receptor like kinases, cell wall strengthening and xenobiotic detoxification enzymes, combined with limited evidence of fungal nutrient acquisition from the plant during symptomless colonisation (Rudd et al., 2015). However, the absence of a resistant variety in the analysis means that our knowledge base remains deficient in regards to characterising

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how longer latent periods are supported by more STB resistant germplasm. In addition, it is significant to note that 167 quantitative trait loci (QTLs) have been identified across nineteen mapping populations (for a comprehensive review of qualitative and quantitative type resistance to STB, see Brown et al., 2015). However the effect these QTLs have on LP length is poorly understood; with a limited number of QTLs controlling LP identified (Ghaffary et al., 2012, Brown et al., 2015). This may be due to mapping studies that locate QTLs usually focusing on disease severity levels. A comprehensive study on the association between LP length and resistance levels of these QTLs would be a significant contribution in regards to determining the overall effect that LP length has on resistance levels.

Cv. Stigg with its pedigree [(Biscay x LW96-2930) x Tanker] has proven along with other synthetic hybrids (Arraiano et al., 2001, Ghaffary et al., 2012, Adhikari et al., 2003), to have a high partially resistant phenotype to STB disease and has the capacity to yield well in areas of high STB pressure and lower optimum fungicide dose (Lynch et al., 2017). While Stigg was removed from the recommended lists due to its inability to attain other agronomic targets, the data presented here endorses its value as a source of STB resistance in breeding programmes. As the durability of resistances depends on both the genotype and the level of selection pressure to the pathogen population (Schilly et al., 2011), it must be noted that cv. Stigg was not widely cultivated in North-West Europe, and therefore the wider durability of its resistance still needs to be fully investigated.

To conclude, this study highlights the agronomic significance of the pre-symptomatic phase in supporting strong partial resistance against *Z. tritici*. In this regard, the synthetically derived variety Stigg displays highly effective field resistance in low, medium and high disease pressure environments. As such, the levels of STB resistance reported here support its

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inclusion in commercial breeding programmes on the condition that its resistance is stacked with other sources of STB resistance to offset the potential for breakdown by the pathogen.

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References

1. Adhikari TB, Anderson JM, Goodwin SB, 2003. Identification and molecular mapping of a gene in wheat conferring resistance to Mycosphaerella graminicola. *Phytopathology* **93**, 1158-64.
2. Armour T, Viljanen-Rollinson S, Chng S, Butler R, Jamieson P, Zyskowski R, 2004. Examining the latent period of Septoria tritici blotch in a field trial of winter wheat. *New Zealand Plant Protection* **57**, 116.
3. Arraiano L, Brading P, Brown J, 2001. A detached seedling leaf technique to study resistance to Mycosphaerella graminicola (anamorph Septoria tritici) in wheat. *Plant Pathology* **50**, 339-46.
4. Arraiano LS, Brown JK, 2016. Sources of resistance and susceptibility to Septoria tritici blotch of wheat. *Molecular Plant Pathology*.
5. Brown JK, Chartrain L, Lasserre-Zuber P, Saintenac C, 2015. Genetics of resistance to Zymoseptoria tritici and applications to wheat breeding. *Fungal Genetics and Biology* **79**, 33-41.

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6. Dooley H, Shaw MW, Mehenni-Ciz J, Spink J, Kildea S, 2016a. Detection of Zymoseptoria triticiSDHI-insensitive field isolates carrying the SdhC-H152R and SdhD-R47W substitutions. *Pest Management Science*, n/a-n/a.
7. Dooley H, Shaw MW, Spink J, Kildea S, 2016b. Effect of azole fungicide mixtures, alternations and dose on azole sensitivity in the wheat pathogen Zymoseptoria tritici. *Plant Pathology* **65**, 124-36.
8. Dooley H, Shaw MW, Spink J, Kildea S, 2016c. The effect of succinate dehydrogenase inhibitor/azole mixtures on selection of Zymoseptoria tritici isolates with reduced sensitivity. *Pest Management Science* **72**, 1150-9.
9. Eyal Z, 1987. *The Septoria diseases of wheat: concepts and methods of disease management*. Cimmyt.
10. Feuillet C, Langridge P, Waugh R, 2008. Cereal breeding takes a walk on the wild side. *Trends in genetics* **24**, 24-32.
11. Fones H, Gurr S, 2015. The impact of Septoria tritici Blotch disease on wheat: an EU perspective. *Fungal Genetics and Biology* **79**, 3-7.
12. Fraaije BA, Cools HJ, Fountaine J, *et al.*, 2005. The Role of Ascospores in Further Spread of QoI-Resistant Cytochrome b Alleles (G143A) in Field Populations of Mycosphaerella graminicola. *Phytopathology* **95**, 933-41.
13. Ghaffary SMT, Faris JD, Friesen TL, *et al.*, 2012. New broad-spectrum resistance to septoria tritici blotch derived from synthetic hexaploid wheat. *Theoretical and Applied Genetics* **124**, 125-42.
14. Goudemand E, Laurent V, Duchalais L, *et al.*, 2013. Association mapping and meta-analysis: two complementary approaches for the detection of reliable Septoria tritici blotch quantitative resistance in bread wheat (Triticum aestivum L.). *Molecular breeding* **32**, 563-84.

Accepted Article

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15. Griffin MJ, Fisher N, 1985. Laboratory studies on benzimidazole resistance in Septoria tritici1. *EPPO Bulletin* **15**, 505-11.
16. Grimmer MK, Van Den Bosch F, Powers SJ, Paveley ND, 2015. Fungicide resistance risk assessment based on traits associated with the rate of pathogen evolution. *Pest management science* **71**, 207-15.
17. Henze M, Beyer M, Klink H, Verreet J-A, 2007. Characterizing meteorological scenarios favorable for Septoria tritici infections in wheat and estimation of latent periods. *Plant Disease* **91**, 1445-9.
18. Hess DE, Shaner G, 1987. Effect of moisture and temperature on development of Septoria tritici blotch in wheat. *Phytopathology* **77**, 215-9.
19. Jess S, Kildea S, Moody A, Rennick G, Murchie AK, Cooke LR, 2014. European Union policy on pesticides: implications for agriculture in Ireland. *Pest management science* **70**, 1646-54.
20. Kajimura T, Mizuno N, Takumi S, 2010. Utility of leaf senescence-associated gene homologs as developmental markers in common wheat. *Plant Physiology and Biochemistry* **48**, 851-9.
21. Kollers S, Rodemann B, Ling J, *et al.*, 2013. Genetic architecture of resistance to Septoria tritici blotch (Mycosphaerella graminicola) in European winter wheat. *Molecular breeding* **32**, 411-23.
22. Kosellek C, Pillen K, Nelson JC, Weber WE, Saal B, 2013. Inheritance of field resistance to Septoria tritici blotch in the wheat doubled-haploid population Solitär× Mazurka. *Euphytica* **194**, 161-76.
23. Li J, Wan HS, Yang WY, 2014. Synthetic hexaploid wheat enhances variation and adaptive evolution of bread wheat in breeding processes. *Journal of Systematics and Evolution* **52**, 735-42.

Accepted Article

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24. Lovell D, Hunter T, Powers S, Parker S, Van Den Bosch F, 2004. Effect of temperature on latent period of septoria leaf blotch on winter wheat under outdoor conditions. *Plant Pathology* **53**, 170-81.

25. Lynch JP, Glynn E, Kildea S, Spink J, 2017. Yield and optimum fungicide dose rates for winter wheat (Triticum aestivum L.) varieties with contrasting ratings for resistance to septoria tritici blotch. *Field Crops Research* **204**, 89-100.

26. Miedaner T, Korzun V, 2012. Marker-assisted selection for disease resistance in wheat and barley breeding. *Phytopathology* **102**, 560-6.

27. O'Driscoll A, Kildea S, Doohan F, Spink J, Mullins E, 2014. The wheat–Septoria conflict: a new front opening up? *Trends in plant science* **19**, 602-10.

28. Reif JC, Zhang P, Dreisigacker S, *et al.*, 2005. Wheat genetic diversity trends during domestication and breeding. *Theoretical and Applied Genetics* **110**, 859-64.

29. Risser P, Ebmeyer E, Korzun V, Hartl L, Miedaner T, 2011. Quantitative trait loci for adult-plant resistance to Mycosphaerella graminicola in two winter wheat populations. *Phytopathology* **101**, 1209-16.

30. Rudd JJ, Kanyuka K, Hassani-Pak K, *et al.*, 2015. Transcriptome and metabolite profiling of the infection cycle of Zymoseptoria tritici on wheat reveals a biphasic interaction with plant immunity involving differential pathogen chromosomal contributions and a variation on the hemibiotrophic lifestyle definition. *Plant physiology* **167**, 1158-85.

31. Sánchez-Vallet A, Mcdonald MC, Solomon PS, Mcdonald BA, 2015. Is Zymoseptoria tritici a hemibiotroph? *Fungal Genetics and Biology* **79**, 29-32.

32. Schilly A, Risser P, Ebmeyer E, *et al.*, 2011. Stability of Adult-plant Resistance to Septoria tritici blotch in 24 European Winter Wheat Varieties Across Nine Field Environments. *Journal of Phytopathology* **159**, 411-6.

Accepted Article

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33. Shaw M, 1990. Effects of temperature, leaf wetness and cultivar on the latent period of Mycosphaerella graminicola on winter wheat. *Plant Pathology* **39**, 255-68.

34. Šíp V, Chrpová J, Palicová J, 2015. Response of Selected Winter Wheat Cultivars to Inoculation. *Czech J. Genet. Plant Breed* **51**, 86-95.

35. Stammler G, Semar M, 2011. Sensitivity of Mycosphaerella graminicola (anamorph: Septoria tritici) to DMI fungicides across Europe and impact on field performance. *EPPO Bulletin* **41**, 149-55.

36. Steinberg G, 2015. Cell biology of Zymoseptoria tritici: Pathogen cell organization and wheat infection. *Fungal Genetics and Biology* **79**, 17-23.

37. Thomas M, Cook R, King J, 1989. Factors affecting development of Septoria tritici in winter wheat and its effect on yield. *Plant Pathology* **38**, 246-57.

38. Torriani SF, Melichar JP, Mills C, Pain N, Sierotzki H, Courbot M, 2015. Zymoseptoria tritici: a major threat to wheat production, integrated approaches to control. *Fungal Genetics and Biology* **79**, 8-12.

39. Viljanen-Rollinson S, Marroni M, Butler R, Deng Y, Armour T, 2005. Latent periods of Septoria tritici blotch on ten cultivars of wheat. *New Zealand Plant Protection* **58**, 256-60.

40. Zadoks JC, Chang TT, Konzak CF, 1974. A decimal code for the growth stages of cereals. *Weed research* **14**, 415-21.

41. Zalewski D, Weber R, Kaczmarek J, 2009. Variation in leaf infection of winter wheat cultivars by fungi of genus Septoria in relation to environmental conditions. *Animal Breeding and Husbandry*, 23.

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Table 1. Agronomic details for the field studies carried out in Carlow, Waterford and Norwich including sowing date, location, sowing date, number of cultivars (cvs) included, fungicide details for rust control around growth stage (GS) applied and respective products and rates as well as date of first disease assessment and respective harvest date.

Location	Sowing date	Number cvs	Fungicide detail		First disease assessment	Harvest date
			GS applied	Products and rates		
Carlow	15.10.13	6	GS30	Amistar at 0.5 l/ha / Corbel at 0.5 l/ha	15.05.14	05.09.14
Waterford	14.10.13	6	GS30	Amistar at 0.5 l/ha / Corbel at 0.5 l/ha	14.05.14	13.08.14
Norwich	23.09.13	4	GS32 GS59	Amistar at 1.0 l/ha / Talius at 0.25 l/ha Amistar at 1.0 l/ha / Talius at 0.25 l/ha	15.05.14	07.08.14
Carlow	24.10.14	7	GS39	Amistar at 0.5 l/ha / Corbel at 0.5 l/ha	29.04.15	08.09.15
Waterford	24.10.14	7	GS39	Amistar at 0.5 l/ha / Corbel at 0.5 l/ha	28.04.15	25.08.15
Norwich	23.09.14	7	GS32 GS59	Amistar at 1.0 l/ha / Talius at 0.25 l/ha Amistar at 1.0 l/ha / Talius at 0.25 l/ha	29.04.15	10.09.15

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Table 2: Mean slope values for fitted logistic curves modelling disease progression on the flag leaf of untreated plots of 7 varieties of winter wheat in Waterford, 2015. PFLP values inputted into the model ranged from 5% to 80%. Statistical significance was tested by Fisher's protected LSD test with cultivars not sharing the same letter significantly different at the P=0.05. Standard error means (SEM) and P-values between cultivars at a given PFLP via one-way ANOVA are also presented.

PFLP	Winter Wheat Cultivars						SEM	LSD	P-value
	Croft	Dunmore	Gator	JB Diego	Kielder	Stigg			
5	0.05^{c}	0.06^{bc}	0.09^{a}	0.07^{abc}	0.00^{d}	0.08^{ab}	0.00	0.02	<0.001
10	0.16^{b}	0.17^{b}	0.23^{a}	0.19^{b}	0.07^{c}	0.17^{b}	0.01	0.03	<0.001
15	0.25^{b}	0.26^{b}	0.34^{a}	0.28^{b}	0.15^{c}	0.24^{b}	0.01	0.05	<0.001
20	0.33^{b}	0.34^{b}	0.45^{a}	0.37^{b}	0.22^{c}	0.30^{b}	0.02	0.07	<0.001
25	0.39^{bc}	0.41^{bc}	0.53^{a}	0.44^{b}	0.28^{d}	0.35^{cd}	0.02	0.08	<0.001
30	0.45^{bc}	0.47^{bc}	0.60^{a}	0.50^{b}	0.34^{d}	0.39^{cd}	0.03	0.09	<0.001
35	0.49^{bc}	0.51^{bc}	0.65^{a}	0.54^{b}	0.38^{d}	0.41^{cd}	0.03	0.10	<0.001
40	0.52^{bc}	0.54^{b}	0.69^{a}	0.57^{b}	0.41^{c}	0.42^{c}	0.03	0.11	<0.001
45	0.54^{bc}	0.56^{b}	0.71^{a}	0.59^{b}	0.43^{c}	0.42^{c}	0.03	0.11	<0.001
50	0.54^{bc}	0.56^{b}	0.71^{a}	0.60^{ab}	0.44^{cd}	0.41^{d}	0.04	0.11	<0.001
55	0.54^{bc}	0.55^{b}	0.70^{a}	0.59^{ab}	0.44^{cd}	0.39^{d}	0.03	0.11	<0.001
60	0.52^{bc}	0.53^{bc}	0.67^{a}	0.56^{ab}	0.42^{cd}	0.35^{d}	0.03	0.10	<0.001
65	0.48^{bc}	0.50^{bc}	0.62^{a}	0.53^{ab}	0.40^{cd}	0.30^{d}	0.03	0.10	<0.001
70	0.44^{bc}	0.45^{bc}	0.56^{a}	0.48^{ab}	0.37^{c}	0.24^{d}	0.03	0.09	<0.001
75	0.38^{bc}	0.39^{bc}	0.48^{a}	0.41^{ab}	0.33^{c}	0.17^{d}	0.02	0.07	<0.001
80	0.31^{bc}	0.32^{bc}	0.38^{a}	0.34^{ab}	0.28^{c}	0.11^{d}	0.01	0.05	<0.001

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Table 3: Mean slope values for fitted logistic curves modelling disease progression on the flag leaf of untreated plots of 7 varieties of winter wheat in Carlow, 2015. PFLP values inputted into the model ranged from 5% to 80%. Statistical significance was tested by Fisher's protected LSD test with cultivars not sharing the same letter significantly different at the P=0.05. Standard error means (SEM) and P-values between cultivars at a given PFLP via one-way ANOVA are also presented.

PFLP	Winter Wheat Cultivars							SEM	LSD	P-value
	Croft	Dunmore	Gallant	Gator	JB Diego	Kielder	Stigg			
5	0.12^{b}	0.07^{c}	0.12^{b}	0.12^{b}	0.14^{b}	0.11^{b}	0.23^{a}	0.01	0.03	<0.001
10	0.27^{b}	0.14^{c}	0.27^{b}	0.26^{b}	0.31^{b}	0.23^{bc}	0.47^{a}	0.02	0.08	<0.001
15	0.40^{bc}	0.21^{d}	0.39^{bc}	0.39^{bc}	0.46^{b}	0.33^{cd}	0.66^{a}	0.04	0.12	<0.001
20	0.51^{bc}	0.27^{d}	0.50^{bc}	0.50^{bc}	0.59^{b}	0.41^{cd}	0.81^{a}	0.05	0.16	<0.001
25	0.61^{bc}	0.32^{d}	0.59^{bc}	0.59^{bc}	0.69^{b}	0.49^{cd}	0.90^{a}	0.06	0.19	<0.001
30	0.69^{bc}	0.36^{d}	0.66^{bc}	0.66^{bc}	0.78^{ab}	0.55^{cd}	0.94^{a}	0.07	0.22	<0.001
35	0.75^{ab}	0.40^{c}	0.72^{ab}	0.71^{ab}	0.84^{a}	0.59^{bc}	0.93^{a}	0.08	0.23	0.003
40	0.80^{ab}	0.42^{c}	0.75^{ab}	0.75^{ab}	0.89^{a}	0.62^{bc}	0.88^{a}	0.08	0.25	0.011
45	0.82^{ab}	0.44^{c}	0.77^{ab}	0.77^{ab}	0.91^{a}	0.64^{bc}	0.77^{ab}	0.08	0.25	0.023
50	0.83^{ab}	0.44^{c}	0.78^{ab}	0.78^{ab}	0.92^{a}	0.64^{bc}	0.62^{bc}	0.08	0.25	0.018
55	0.82^{ab}	0.44^{c}	0.76^{ab}	0.76^{ab}	0.90^{a}	0.63^{bc}	0.41^{c}	0.08	0.25	0.003
60	0.80^{ab}	0.43^{cd}	0.73^{ab}	0.73^{ab}	0.86^{a}	0.60^{bc}	0.19^{d}	0.08	0.25	<0.001
65	0.75^{ab}	0.42^{cd}	0.68^{ab}	0.68^{ab}	0.81^{a}	0.56^{bc}	0.26^{d}	0.07	0.22	<0.001
70	0.69^{ab}	0.39^{c}	0.61^{ab}	0.61^{ab}	0.73^{a}	0.50^{bc}	0.00^{d}	0.06	0.19	<0.001
75	0.61^{a}	0.35^{c}	0.53^{ab}	0.53^{ab}	0.63^{a}	0.43^{bc}	0.51^{ab}	0.05	0.16	0.014
80	0.52^{a}	0.31^{b}	0.43^{ab}	0.43^{ab}	0.51^{a}	0.35^{b}	0.42^{ab}	0.04	0.12	0.011

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Table 4: Degree day values derived from fitted logistic curves modelling disease progression on the flag leaf of untreated plots of 7 varieties of winter wheat in Waterford, 2015. PFLP values inputted into the model ranged from 5% to 80%. Statistical significance was tested by Fisher's protected LSD test with cultivars not sharing the same letter significantly different at the P=0.05. Standard error means (SEM) and P-values between cultivars at a given PFLP via one-way ANOVA are also presented.

PFLP	Winter Wheat Cultivars						SEM	LSD	P-value	Difference in mean cultivar ^{o}day v. ^{o}day Stigg
	Croft	Dunmore	Gator	JB Diego	Kielder	Stigg				
5	609^{a}	663^{b}	639^{ab}	667^{b}	---	783^{c}	11.22	33.11	<.001	138(17.67%)
10	660^{a}	709^{b}	683^{ab}	709^{b}	640^{a}	822^{c}	11.51	33.61	<.001	141 (17.25%)
15	686^{a}	734^{b}	704^{ab}	733^{b}	688^{a}	845^{c}	10.42	30.42	<.001	136 (16.09%)
20	704^{a}	752^{b}	718^{ab}	749^{b}	717^{ab}	863^{c}	10.06	29.35	<.001	135 (15.64%)
25	718^{a}	766^{b}	729^{ab}	763^{b}	738^{ab}	878^{c}	10.03	29.27	<.001	135 (15.39%)
30	731^{a}	779^{b}	738^{ab}	775^{b}	755^{ab}	892^{c}	10.19	29.74	<.001	136 (15.29%)
35	742^{a}	790^{b}	747^{ab}	786^{ab}	770^{ab}	904^{c}	10.47	30.57	<.001	137 (15.15%)
40	752^{a}	800^{a}	754^{a}	795^{a}	784^{a}	916^{b}	10.85	31.67	<.001	139 (15.17%)
45	762^{a}	810^{a}	762^{a}	805^{a}	797^{a}	927^{b}	11.31	33.00	<.001	139 (15.08%)
50	772^{a}	820^{a}	769^{a}	814^{a}	810^{a}	939^{b}	11.84	34.56	<.001	142 (15.12%)
55	782^{a}	830^{a}	777^{a}	824^{a}	822^{a}	952^{b}	12.47	36.40	<.001	145 (15.23%)
60	792^{a}	840^{a}	784^{a}	833^{a}	835^{a}	966^{b}	13.23	38.62	<.001	149 (15.44%)
65	802^{a}	850^{a}	792^{a}	844^{a}	848^{a}	982^{b}	14.21	41.48	<.001	154 (15.76%)
70	814^{a}	862^{a}	801^{a}	855^{a}	862^{a}	1002^{b}	15.67	45.73	<.001	163 (16.28%)
75	827^{a}	874^{a}	810^{a}	867^{a}	878^{a}	1031^{b}	19.11	55.77	<.001	179 (17.43%)
80	843^{a}	890^{a}	822^{a}	882^{a}	896^{a}	1092^{b}	26.83	55.51	<.001	225 (20.64%)

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Table 5: Degree day values derived from fitted logistic curves modelling disease progression on the flag leaf of untreated plots of 7 varieties of winter wheat in Carlow, 2015. PFLP values inputted into the model ranged from 5% to 80%. Statistical significance was tested by Fisher's protected LSD test with cultivars not sharing the same letter significantly different at the P=0.05. Standard error means (SEM) and P-values between cultivars at a given PFLP via one-way ANOVA are also presented.

PFLP	Winter Wheat Cultivars							SEM	LSD	P-value	Difference in mean cultivar ^{o}day v. ^{o}day Stigg
	Croft	Dunmore	Gallant	Gator	JB Diego	Kielder	Stigg				
5	821^{bc}	713^{a}	716^{a}	707^{a}	818^{c}	705^{ab}	937^{d}	21.48	62.22	<.001	190 (20.3%)
10	854^{b}	761^{a}	744^{a}	748^{a}	847^{b}	743^{a}	952^{c}	18.42	53.36	<.001	169 (17.7%)
15	873^{b}	790^{a}	760^{a}	772^{a}	864^{b}	766^{a}	962^{c}	16.67	48.28	<.001	157 (16.4%)
20	887^{b}	811^{a}	772^{a}	790^{a}	877^{b}	784^{a}	969^{c}	15.43	44.71	<.001	148 (15.4%)
25	898^{c}	828^{ab}	781^{a}	805^{a}	887^{bc}	798^{a}	976^{d}	14.48	41.94	<.001	143 (14.7%)
30	908^{c}	843^{ab}	790^{a}	818^{a}	896^{bc}	810^{a}	981^{d}	13.70	39.69	<.001	136 (13.9%)
35	916^{c}	856^{bc}	798^{a}	830^{ab}	904^{c}	822^{ab}	987^{d}	13.05	37.79	<.001	132 (13.4%)
40	924^{c}	869^{bc}	805^{a}	841^{ab}	912^{c}	832^{ab}	993^{d}	12.48	36.24	<.001	129 (13%)
45	932^{c}	881^{bc}	812^{a}	851^{ab}	919^{c}	842^{ab}	1000^{d}	11.72	33.96	<.001	127 (12.7%)
50	940^{c}	893^{bc}	818^{a}	862^{ab}	926^{c}	853^{ab}	1007^{d}	11.58	33.55	<.001	125 (12.4%)
55	947^{c}	904^{bc}	825^{a}	872^{ab}	933^{c}	863^{ab}	1018^{d}	11.28	32.69	<.001	127 (12.5%)
60	955^{c}	916^{bc}	832^{a}	883^{ab}	940^{c}	873^{ab}	1037^{d}	11.19	32.42	<.001	137 (13.2%)
65	962^{c}	928^{bc}	840^{a}	894^{ab}	948^{c}	884^{a}	---	11.43	33.38	<.001	---
70	971^{d}	940^{cd}	848^{a}	906^{bc}	956^{d}	896^{ab}	---	11.18	32.64	<.001	---
75	980^{d}	954^{cd}	857^{a}	920^{bc}	966^{cd}	910^{ab}	---	11.17	32.59	<.001	---
80	990	969^{d}	868^{cd}	936^{a}	976^{bc}	926^{ab}	---	---	---	<.001	---

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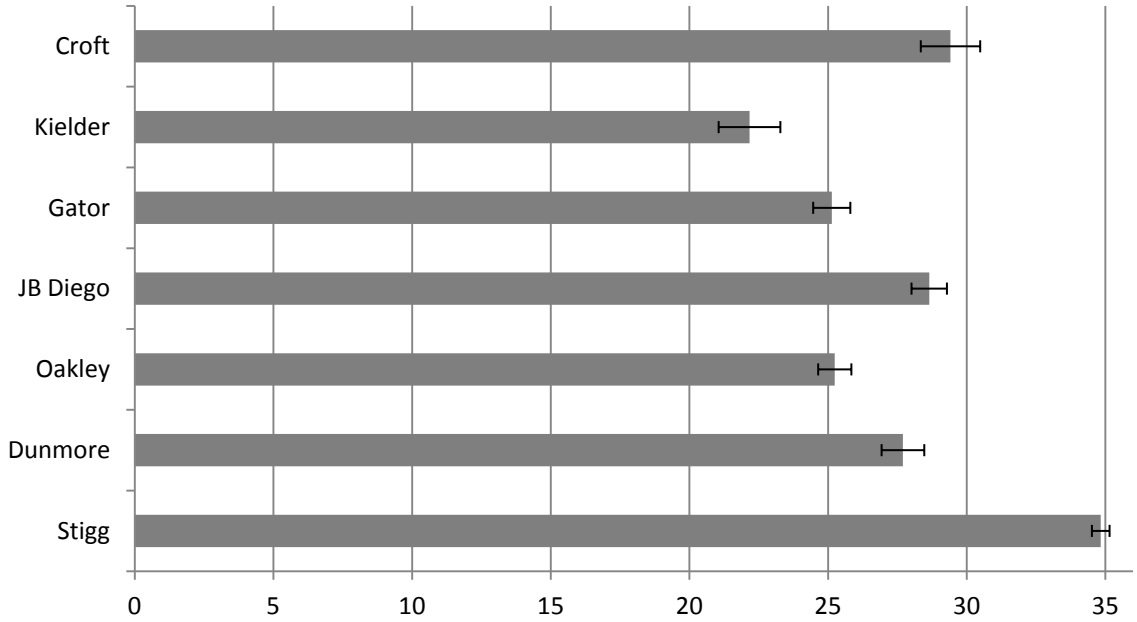

Figure 1. Glasshouse based evaluation of cultivar (n = 7) specific latent periods. Latent period was characterized as the number of days post-infection after which the first lesions bearing pycnidia appeared. Statistical significance was tested by the Tukey Test, with cultivars not sharing the same letter significantly different at the P=0.05 level. Error bars represent plus and minus SEM.

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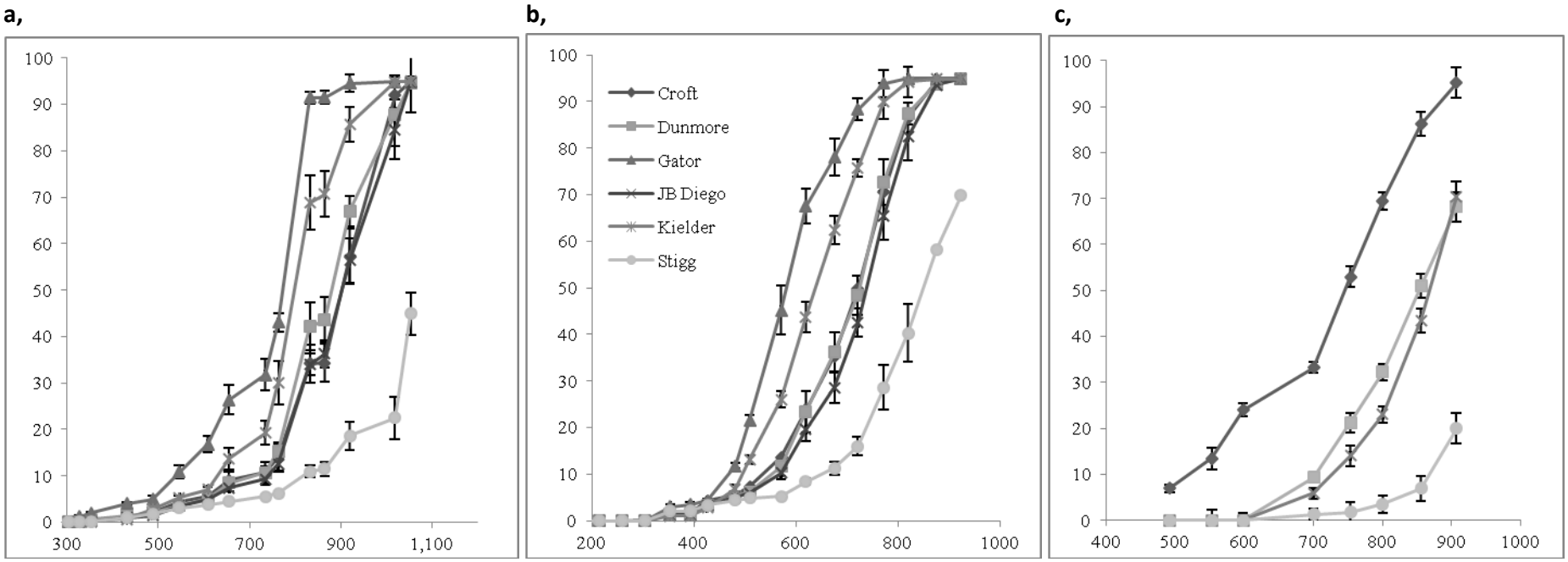

Figure 2. Mean progression of Septoria tritici blotch disease on flag leaves of untreated plots of winter wheat cvs. Croft, Dunmore, Gallant, Gator, JB Diego, Kielder and Stigg grown in Waterford (a), Carlow (b) and Norwich (c) locations in the 2013-2014 season. The Y axis represents PFLP, X axis represent ^{o}Days. Error bars represent plus and minus SEM.

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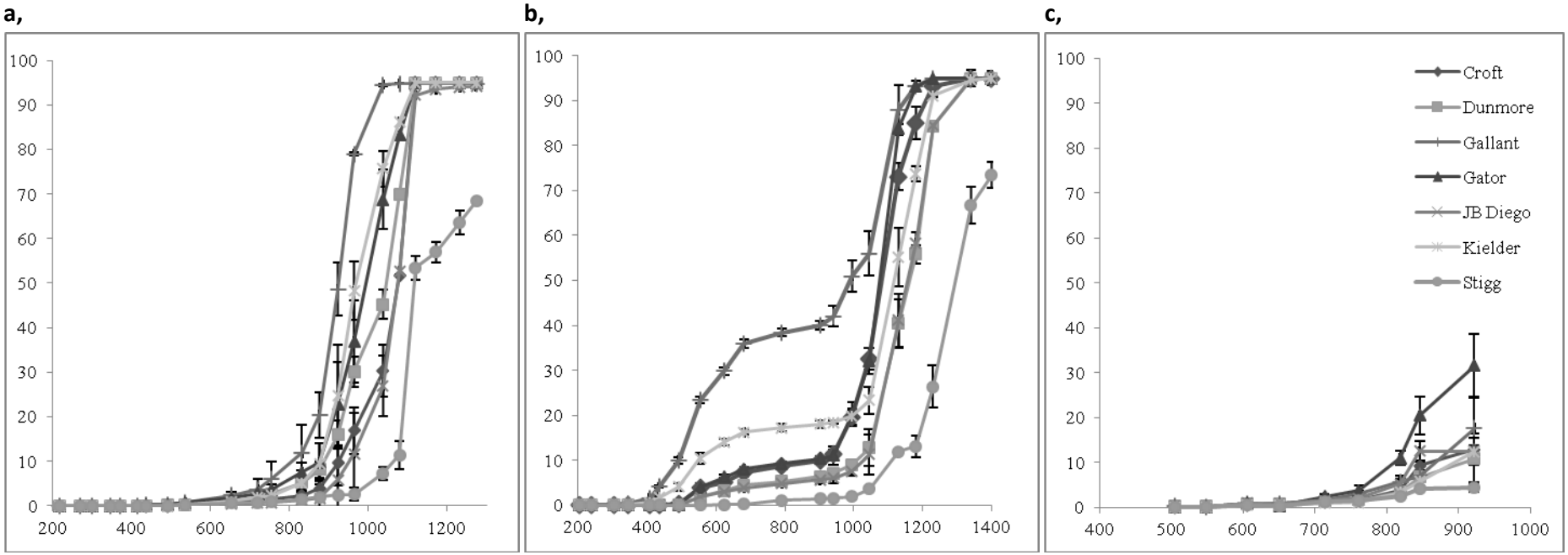

Figure 3. Mean progression of Septoria tritici blotch disease on flag leaves of untreated plots of winter wheat cvs. Croft, Dunmore, Gallant, Gator, JB Diego, Kielder and Stigg grown in Waterford (a), Carlow (b) and Norwich (c) locations in the 2014-2015 season. The y axis represents PFLP, x axis represent ^{o}Days. Error bars at the top of each graph represent plus and minus SEM.

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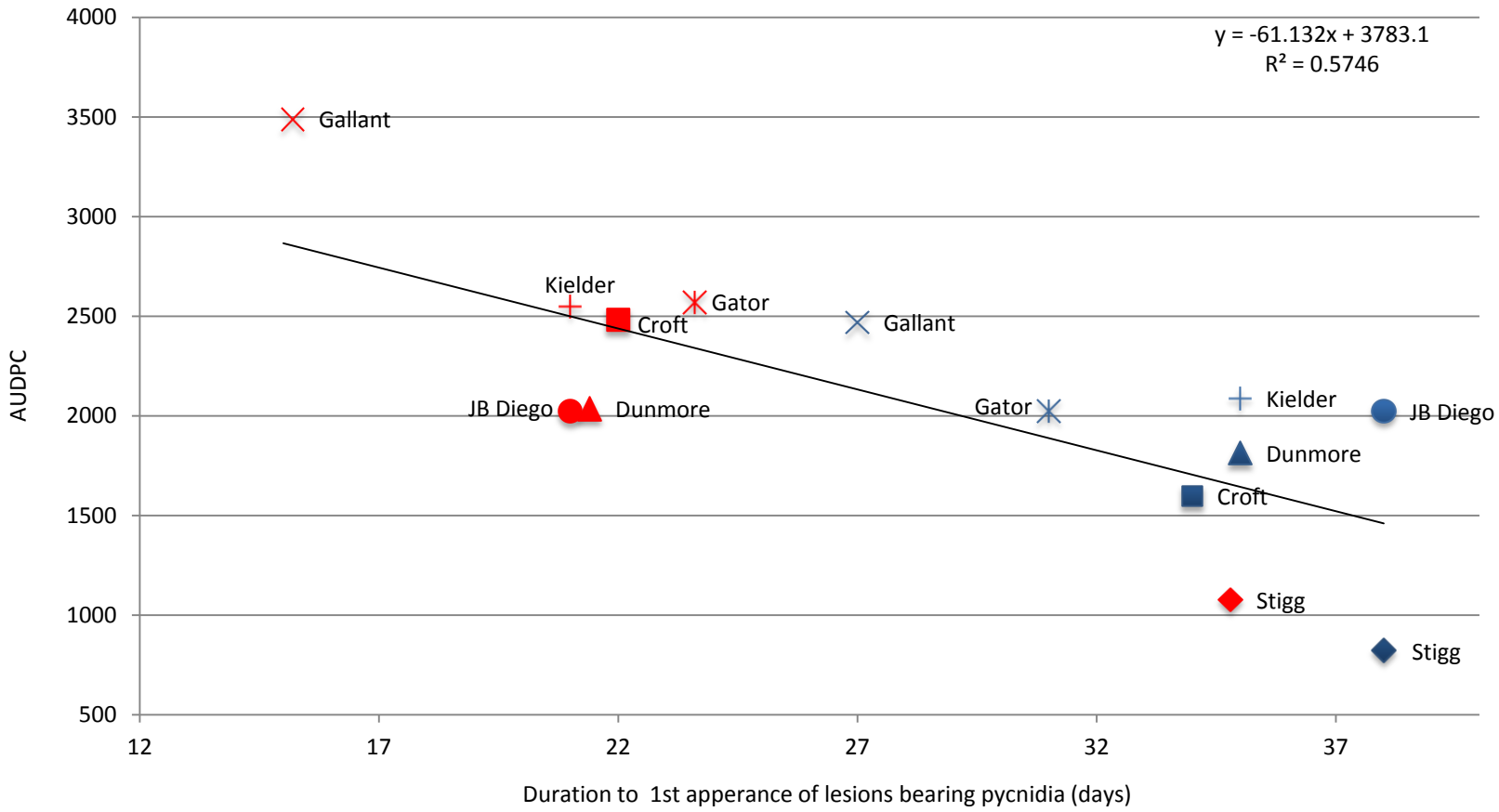
Figure 4. Association between individual cultivar area under disease progress curve (AUDPC) values and the duration before the 1st appearance of pycnidia on the flag leaf (days) was recorded for Stigg, Croft, Dunmore, JB Diego, Kielder, Gator and Gallant, cultivated at Waterford (red) and Carlow (blue) in 2015.



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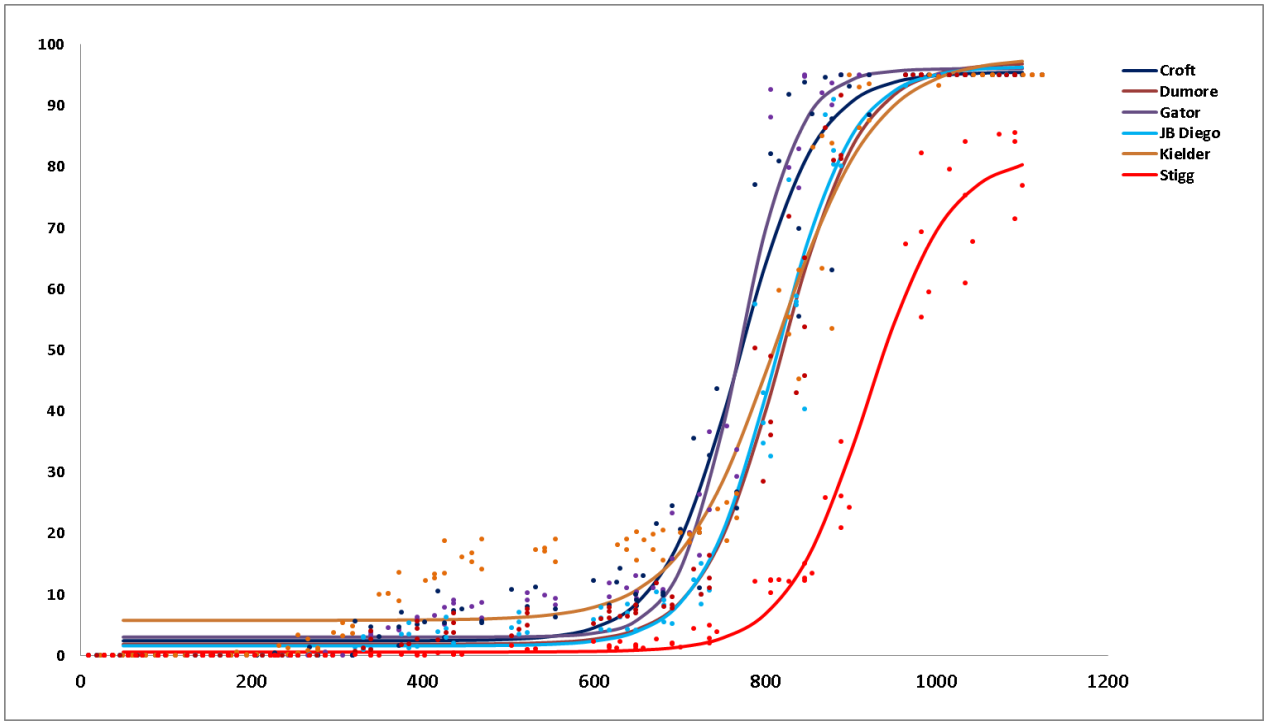
a,



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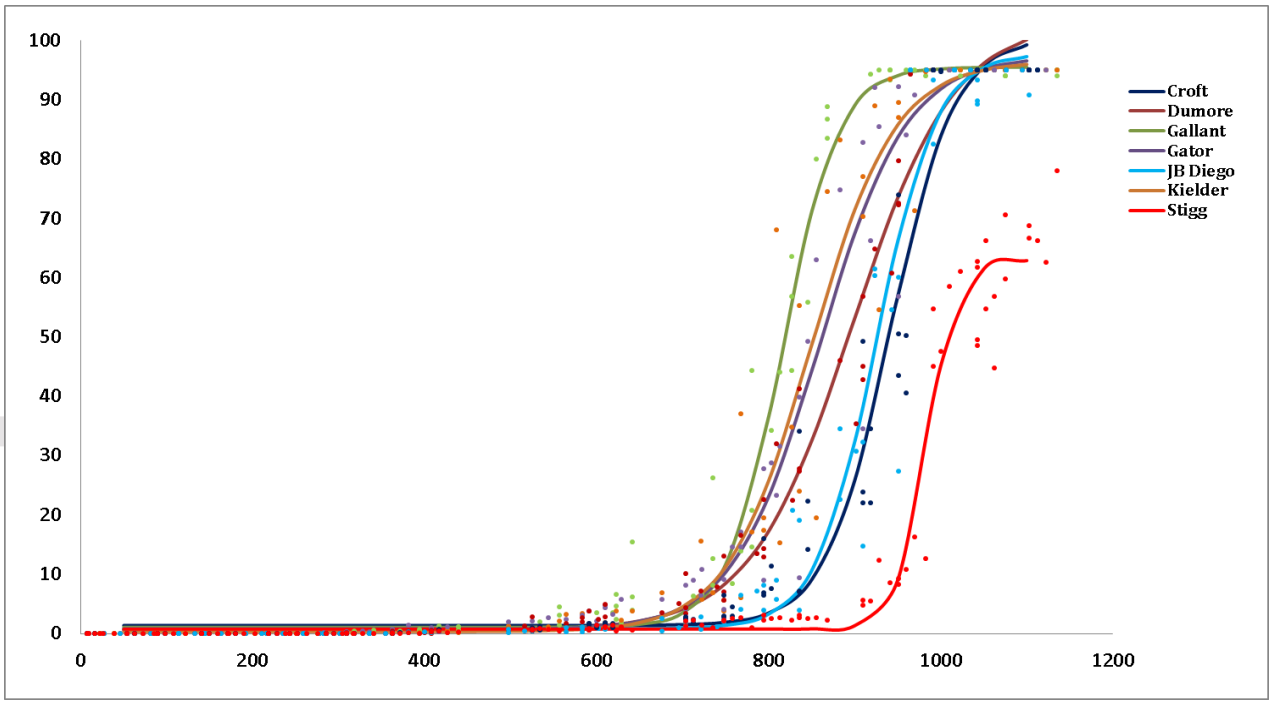

Figure 5. Logistic curves fitted to the mean flag leaf derived STB disease scores of untreated plots of winter wheat cvs Croft, Dunmore, Gator, JB Diego, Kielder, Gallant and Stigg, grown in Waterford (a) and Carlow (b) in 2015. The y axis represents PFLP, x axis represent °Days. Individual data points on these figures represent PFLP and equivalent °Day values of each replicate plot per variety. For each variety there were 5 replicates plots within which 10 plants were randomly tagged for repeat assessment.

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