Van Den Bosch, F., Smith, J., Wright, P., Milne, A. E., Van Den Berg, F., Kock-Appelgren, P., Foulkes, J. and Paveley, N. 2021. Maximizing realized yield by breeding for disease tolerance: A case study for Septoria tritici blotch. *Plant Pathology.* https://doi.org/10.1111/ppa.13509

Received: 30 June 2021 | Accepted: 29 October 2021

DOI: 10.1111/ppa.13509

ORIGINAL ARTICLE

Plant Pathology WILEY

Maximizing realized yield by breeding for disease tolerance: A case study for Septoria tritici blotch

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Funding information

Department for Environment, Food and Rural Affairs of the United Kingdom; Biotechnology and Biological Sciences Research Council (BBSRC)

Abstract

Disease-tolerant cultivars maintain yield in the presence of disease. When disease intensity is high, they can improve a grower's net return compared to less tolerant cultivars. Many authors report a trade-off, whereby higher fully protected yields are correlated with a lower disease tolerance. We analyse the question for breeders: to what extent should they breed for tolerance when it compromises maximizing fully protected yield? Field trials with 147 progeny from five parental crosses of wheat were used to measure yield and tolerance under a range of disease intensities from Septoria tritici blotch (STB; causal organism *Zymoseptoria tritici*) at a range of sites and seasons. The data define the variation for these traits from which breeders can select. A simple data-driven descriptive model was used to calculate the combination of tolerance and fully protected yield that maximizes actual yield for any given level of disease—quantified by loss of healthy canopy area duration (HAD-loss). This model was combined with data on the year-to-year variability of HAD-loss in the UK to calculate the tolerance and fully protected yield that maximizes the mean actual yield. We found that even when an effective fungicide treatment programme is applied, breeding for tolerance increases the mean actual yield. Some commercially available cultivars were found to have a level of tolerance that leads to yields close to the maximum yield in the presence of disease, others had a lower tolerance leading to suboptimal yields.

KEYWORDS

breeding for disease tolerance, healthy area duration, maximizing realized yield, yield tolerance trade-off

1 | INTRODUCTION

Disease tolerance is a heritable trait of crop cultivars, quantified as the ability to maintain yield in the presence of disease (Schafer, 1971). In the presence of disease symptoms, a more tolerant cultivar will produce yields closer to its yield potential than a less tolerant cultivar. This is distinct from partial disease resistance, which is also referred to as tolerance by some authors. Tolerant cultivars could therefore improve a grower's net financial return compared to a less tolerant cultivar. Yet, tolerance is not a priority breeding target in most plant breeding programmes. The top-ranked breeding target is usually grain yield (Anonymous, 2021; Braun et al., 1997) when grown in high-input production systems, including an effective foliar-applied fungicide programme.

Breeders may assume that an effective fungicide treatment programme will reduce disease to a low severity, and that tolerance is not a necessary attribute of a cultivar. However, even under intensive fungicide treatment programmes, and with current levels of host resistance, disease frequently develops to a level that affects yield. Loss of effective fungicides due to the development of fungicide resistance and regulatory changes reducing the number of fungicide products available, and loss of effective host resistance to the development of virulence breaking crop resistance, exacerbate those yield losses (Singh et al., 2016). Breeding for tolerance could, therefore, improve yields. The benefits of tolerance should be even greater in resource-poor farming systems if fungicides are not available or affordable. Although tolerance was reported in the 1970s (Ziv & Eyal, 1978), progress towards understanding and exploiting the mechanisms that confer tolerance has been slow.

Several authors have measured or inferred a negative correlation between tolerance and fully protected yield (van den Berg et al., 2017; Bingham & Topp, 2009; Foulkes et al., 2006; Kramer et al., 1980; Parker et al., 2004), though in a recent study of Argentinian cultivars such a trade-off is not found (Castro & Simon, 2016). “Fully protected yield” is used here in the sense of the yield obtained when strong crop protection measures are used to alleviate biotic stress (see Table 1 for yield nomenclature). It is not known to what extent the trade-off between tolerance and fully protected yield is causal or might be ameliorated by further breeding. Given that this association exists currently in most cases investigated, a key question is whether including tolerance as a breeding target, even if this reduces the fully protected yield to some extent, will result in a higher actual yield in the presence of disease. The analysis reported here explores this question using field data for *Zymoseptoria tritici* on winter wheat in the UK.

To focus the analysis, we define as the breeding goal a cultivar that under a given disease control regime gives, averaged over a run of years, the largest actual yield. A method is presented to calculate the level of tolerance and the fully protected yield that achieves this breeding goal.

TABLE 1 Yield nomenclature

Term	Description
Potential yield	A theoretical maximum yield for an environment.
Yield potential	The yield of a cultivar grown in an environment to which it is adapted, with non-limiting resources (water and nutrients) and biotic and abiotic stresses controlled (Senepati & Semenov, 2020 and references cited therein).
Fully protected yield	The yield obtained at a specific location when all available crop protection tactics are used to alleviate the stresses caused by pathogens, invertebrate pests, and weeds.
Actual yield	The yield achieved when disease control is incomplete and recommended pest and weed management programmes (i.e., those that are available in practice and implemented to an economically optimal extent) are used.
Yield loss	The reduction in yield caused by a single pathogen.

2 | MATERIALS AND METHODS

2.1 | Overview

Two data sets were used, one to quantify the association between fully protected yield and tolerance, further described in the section 2.2, and a data set to quantify HAD-loss, further described in the section 2.3. To quantify the association between fully protected yield and tolerance, populations of progeny from several parental crosses of winter wheat resulting in a large set of wheat lines were used to estimate fully protected yield (under an intensive fungicide programme) and tolerance. A scatter plot for the relationship between tolerance and fully protected yield quantified the available breeding space.

Although tolerance has in most studies been quantified from the slope of the relationship between area under disease progress curve and grain yield (Inglese & Paul, 2006; Kramer et al., 1980), this measure is very sensitive to site and seasonal variations as well as difficulties distinguishing diseased from senesced leaf area. Parker et al. (2004) showed that the slope of the regression line of yield on healthy area duration (HAD) for a cultivar or line provides a more reliable measure of tolerance. Variation in HAD for each cultivar or line was obtained by either abstaining fungicide treatment or random variation in disease severity between plots. This tolerance measure has a dimension of tonne per hectare per unit of HAD-loss and can thus easily be combined with fully protected yield to calculate the contribution of tolerance to mean actual yield under given levels of disease (quantified by the HAD-loss caused).

A simple data-driven descriptive model was used to calculate the combination of tolerance and fully protected yield that maximizes actual yield for any given HAD-loss level. Disease, and hence HAD-loss, varies between years. Data on the year-to-year variability of HAD-loss in the UK was therefore used to calculate the tolerance and fully protected yield that maximizes the mean actual yield, which is the defined breeding goal.

2.2 | Data on the yield-tolerance breeding space

We used progeny from five parental crosses, developed as doubled-haploid (DH) mapping populations: Avalon × Cadenza (A × C), Cadenza × Lynx (C × L), Line 14 × Rialto (L14 × R), Xi19 × synthetic hexaploid wheat (Xi19 × SHW), and Line 8 × Rialto (L8 × R), to measure yield and tolerance. These mapping populations were chosen because previous work suggested that a wider range of tolerance would be found in offspring than we had identified in previous material. Data from a subset of this material has been reported previously by Collin et al. (2018). A × C and C × L populations were used because the parents are known to contrast for source and sink traits such as green leaf area index (GLAI), extinction coefficient value, number of grains per ear, flag leaf size, and posture. The L14 × R and L8 × R populations were developed by the International Maize and Wheat Improvement Centre (CIMMYT). L14 is a spring wheat large-ear phenotype advanced line expressing traits such as high assimilate partitioning to ear and high fertile florets per ear, and Rialto is a UK winter wheat variety that has high radiation-use efficiency and stem soluble carbohydrates. In addition, L14 and Rialto contrast for the presence/absence of the *TinlA* allele, which controls tiller inhibition. L8 is also a large-ear phenotype CIMMYT spring wheat advanced line derived in a wide-crossing programme involving *Agropyron elongatum*, *Triticum polonicum*, and *Triticum aestivum* to create restructured hexaploid wheat plant types exploiting heterosis. The mapping populations were prescreened and a maximum of 50 lines from each population were included in the main field experiments. Lines were excluded from the field experiments if they developed <10% Septoria tritici blotch (STB), were >100 cm tall, yielded <5 t/ha, were extremely early or late flowering, or had <10,000 or >18,000 grains/m^2.

For comparison, in some site-years we also planted the parent cultivars and other commercially available elite cultivars. Table 2 summarizes the lines and cultivars used in each site-year. Over eight site-years, a total of 257 site-year-line combinations were completed. We used the same experimental methods as described by Foulkes et al. (2006) and refer the reader to that paper for details. Here we only give sufficient information on the method to follow the paper.

Each experiment used a randomized split-plot design with three replicates. There were two fungicide treatments to create differences in HAD, that is, an intensive fungicide programme to control foliar disease and an untreated control. Nontarget diseases such as rusts, mildew, eyespot, and fusarium head blight were controlled in untreated plots by applying combinations of pyraclostrobin (Comet 0.5 L/ha), proquinazid (Talius 0.2 L/ha), cyflufenamid (Cyflamid 0.25 L/ha), and cyprodinil (Unix 1 kg/ha) at the key timings. Fungicide-protected plots received the same programme as the untreated plots with the addition of epoxiconazole and metconazole coformulation (Brutus 2 L/ha) and chlorothalonil (Bravo 1 L/ha) to control septoria. All applications remained within the recommended label rate. A robust weed and invertebrate control programme was applied to all plots. For example, glyphosate (Clinic Ace 3.5 L/ha) was applied as a pre-emergence herbicide. Broad-leaved weeds and grasses were controlled by a late November tank-mix application of diflufenican (Diflanil 500 SC 0.06 L/ha), diflufenican + flurtamone (Graduate 0.2 L/ha), pendimethalin (PDM 330 EC 1.5 L/ha), and flufenacet + pendimethalin (Trooper 1.75 L/ha). A further herbicide application of pyroxsulam + florasulam (Broadway Star 0.265 L/ha) was made in March. The insecticide lambda-cyhalothrin (Markate 50 0.1 5 L/ha) was applied to all plots in November and June, and molluscicide methiocarb (Decoy Wetex 5 kg/ha) was applied in November.

The yield of all plots was measured using a plot combine harvester and grain yield was corrected to 85% dry matter. Yield data from fungicide-treated plots were used as measures of the fully protected yields of the lines. GLAI was assessed as the planar green leaf area per unit ground area on three occasions: GS59, GS59 + 14 days, and GS59 + 28 days. Where the season was predicted to be shortened due to very warm dry weather, the measurement interval was reduced to every 10 days. The date of canopy senescence was recorded for

TABLE 2 Number of wheat lines of crosses used in each site year, and commercially available cultivars used in each site year

Year	Site	A × C	C × L	L14 × R	L8 × R	Xi19 × SHW	Avalon	Cadenza	Lynx	Option	Xi19	Rialto	Malaca	Claire
2006	Rosemaund		12					✓	✓					
2012	Panniers	40	10											
2012	Gatley	40	9											
2012	Rosemaund		10	38								✓		
2013	Rosemaund		6		30		✓			✓	✓	✓	✓	✓
2014	Rosemaund I	2	4	8	2		✓	✓	✓	✓	✓	✓	✓	✓
2014	Rosemaund II					19	✓			✓	✓		✓	✓
2014	Cardigan					27	✓			✓	✓		✓	✓

Note: A × C: Avalon × Cadenza; C × L: Cadenza × Lynx; L14 × R: Line 14 × Rialto; Xi19 × SHW: Xi19 × synthetic hexaploid wheat; L8 × R: Line 8 × Rialto.

each individual plot and was defined as being the date at which the percentage green leaf area of the canopy was less than 15% of full canopy size (equating to a GLAI of <1). This occurred at approximately GS83 (early dough). Using these GLAI data, HAD was calculated using the trapezium rule, over the top four leaves between GS59 and canopy senescence. Note that this is a different time interval and number of leaves than used by Parker et al. (2004) and Foulkes et al. (2006) to calculate HAD. The reasons for this change is that previously we have found little difference between fungicide treatments until GS39. Combined with reduction of costs, this made us decide to work with GS59. Plotting yield as a function of HAD (Figure 1) allowed the calculation of tolerance as the slope of a straight line fitted to the data using least squares. These methods generated fully protected yield and tolerance measurements for 179 line-site-years.

Steeper slopes are due to greater yield losses with decreasing HAD, indicating a lower tolerance. This means that the larger the value of the tolerance slope measure, the less tolerant the cultivar, with tolerance slope measures of zero conferring absolute tolerance to disease. For convenience of interpretation, we plot values of tolerance in reverse order on the chart axes, so that points higher along the axis have greater tolerance.

2.3 | Data on HAD-loss

Calculating the effect of tolerance on actual yield under field conditions requires data on HAD-loss for a range of sites and seasons in cases where a full fungicide treatment programme is applied. For comparison we also calculated the HAD-loss in the absence of fungicide treatments. These calculations were performed using the data sets described in te Beest et al. (2009) on the epidemics of *Z. tritici*. We refer the reader to that paper for details.

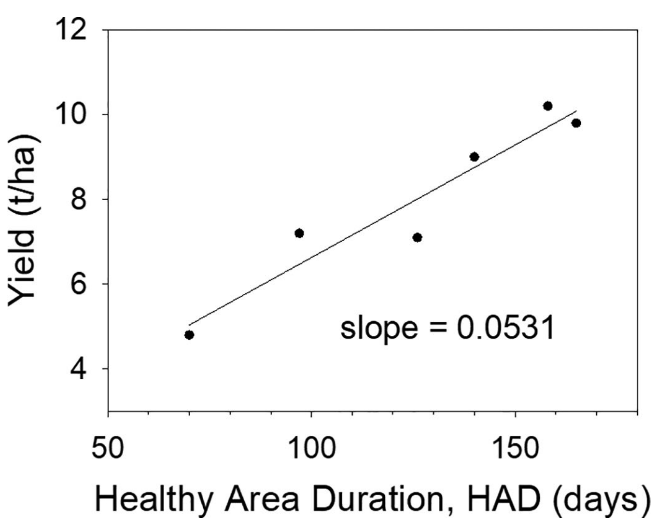

FIGURE 1 Linear regression of a set of field data on yield as function of the Healthy Area Duration, HAD. The slope of the line is the measure of tolerance. The larger the slope of the line the lower the tolerance, the smaller the slope of the line the higher the tolerance

The data set comprises 120 site-years from experiments undertaken in the UK between 1998 and 2002. Plots with commercially available elite cultivars were grown in three replicates. Treatments were either an intensive foliar applied fungicide programme or an untreated control. We refer to Parker et al. (2004, Table 2) for the fungicide treatment programmes used. Assessments were performed at 10-day intervals from GS31 until senescence. GLAI and diseased symptom area index (SAI) were assessed, with the latter measured as the leaf area affected by *Z. tritici* per unit ground area, excluding naturally senesced area.

HAD-loss in the presence of a fungicide treatment programme was calculated in four steps: (a) scatter plots of treated and untreated SAI versus GLAI were generated of all replicate values for each variety and assessment date, (b) using least squares, a straight line was fitted to the data, (c) extrapolating this line to SAI = 0 gives an estimate of the GLAI in the absence of disease, and (d) using these data, HAD over the top four leaves from GS59 until senescence in the absence of disease was calculated. HAD was also calculated using the GLAI of the treated plots. The difference between the HAD in the absence of disease and HAD of the treated plots gives an estimate of the HAD-loss when a full fungicide treatment programme was used.

HAD in the absence of disease, as calculated above, gives the absolute maximum HAD. The HAD in the untreated plots gives the HAD under full disease exposure. The difference of these two quantities is the HAD-loss when no fungicide treatments are applied.

Exponential distributions, $P(\mathrm{HAD}_{\mathrm{loss}})$, were fitted to the HAD-loss data using least squares, omitting the few negative values of HAD-loss.

2.4 | The model

The 179 site-year-lines for which a tolerance value was derived were used to generate a scatter plot of fully protected yield versus tolerance. Data from lines with yields smaller than 7 t/ha were omitted, as lines with such low yields are not of practical relevance in north-west Europe. An enveloping line was fitted around the data points describing the fully protected yield for each value of tolerance (Figure 2) and forms the basis of our assessment of optimal fully protected yield-tolerance combinations.

Published methods for fitting enveloping lines around data sets (Lark & Milne, 2016; Milne & Lark, 2006) require a dense concentration of data points near the enveloping line. Our data set did not meet this criterion. Therefore, an alternative method was applied. A convex hull was constructed around the data using the Jarvis (1973) algorithm. The points supporting the convex hull are removed and those describing the relationship between tolerance and maximum fully protected yield stored in a separate data set. The process is repeated twice more, each time the data points supporting the relationship are added to the separate data set. A line is fitted to the set of data points resulting from this process. The upper part of the envelope was found to have a smaller slope than the lower part, and to avoid negative values of the tolerance we fitted polynomials in ln(tolerance) versus fully protected yield.

Referring to Figure 1, the relationship between actual yield, Y_A, fully protected yield, Y_F, and HAD is given by

$$Y_A = Y_F (A + \alpha \mathrm{HAD}). \tag{1}$$

where A is a constant and α is intolerance. When HAD equals the fully protected HAD, HAD_F, the actual yield equals the fully protected yield, $Y_A = Y_F$. Equation 1 then becomes

$$Y_A = Y_F \left(1 - \alpha \left(\mathrm{HAD}_F - \mathrm{HAD}\right)\right). \tag{2}$$

Rewriting this relationship we find

$$\alpha = \frac{1}{\mathrm{HAD}_F - \mathrm{HAD}} \left(1 - \frac{Y_A}{Y_F}\right). \tag{3}$$

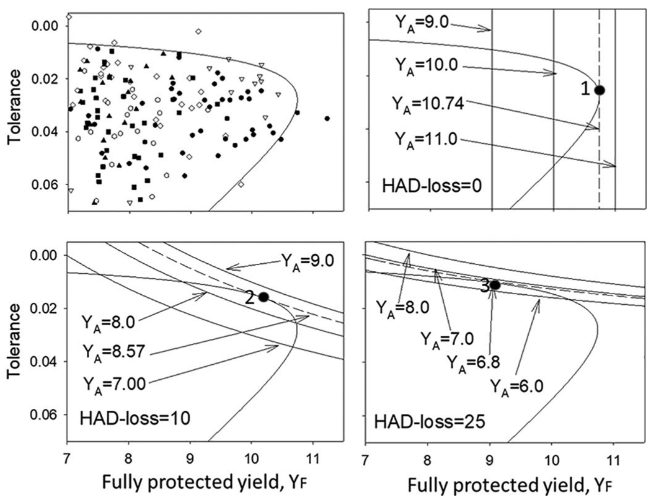

FIGURE 2 Tolerance as a function of fully protected yield, Y_F. Note that the tolerance axis is inverted with smaller values above larger values. This enables us to interpret the tolerance axis as increasing tolerance higher-up on the axis. Top left: Tolerance and yield data of the near-isogenic lines, NILs, assessed in the field (Table 2). Only data points with fully protected yield >7 t/ha are presented. Each dot is a NIL-site-year. The drawn line is the line enveloping the data. The yield-tolerance space inside the envelope represents the combinations of yield and tolerance attainable by breeding. Top right: The enveloping line and lines of equal actual yield, Y_A. In this figure the HAD-loss equals zero, meaning there is no disease. The actual yield line touching the envelope, the dashed line, is the line with the largest actual yield attainable by breeding. The point where the envelope touches the line is the combination of fully protected yield and tolerance that maximizes the realized yield. Bottom left: The enveloping line and lines of equal actual yield for a HAD-loss of 10. The dashed line represents the maximum actual yield line. The point where the line touches the enveloping line is the breeding target (combination of yield and tolerance) for which the actual yield is maximized. Bottom right: Same as bottom left but then for a HAD-loss of 25. In each panel the breeding target, the optimal combination of tolerance and yield, is marked with a dot and a number. These dots and numbers reappear in Figure 3

and HAD_F − HAD is the HAD-loss due to disease, HAD_{loss}. Plotting Equation 3 in Figure 3 gives lines of equal actual yield, Y_A. These lines of equal Y_A and the enveloping line can be used to determine the optimal combination of fully protected yield, Y_F, and tolerance, α. See section 3 for a further explanation.

Using the enveloping line fitted to the tolerance-fully protected yield data and Equation 3, we calculate the tolerance level and the fully protected yield that leads to the maximum actual yield for a given HAD-loss, $T(\mathrm{HAD}_{loss})$. Using the HAD-loss probability densities as derived from the data, as discussed above, $P(\mathrm{HAD}_{loss})$, the mean tolerance value that maximizes actual yield is calculated from

$$E(\alpha) = \int_0^{\mathrm{HAD}_F} P\left(\mathrm{HAD}_{loss}\right) T\left(\mathrm{HAD}_{loss}\right) d\mathrm{HAD}_{loss}. \tag{4}$$

To further assess the effect of cultivar resistance on the optimal tolerance, the HAD-loss data were grouped according to the STB resistance rating as published in the recommended list of winter wheat cultivars. A function was fitted describing the effect of resistance rating on the mean HAD-loss, both for the cases where no fungicides are used and the cases where a full fungicide treatment programme is applied.

Finally, the optimal tolerance was compared to the experimentally estimated tolerance of the commercially available elite cultivars included in the experiments. For each of these cultivars we calculate the percentage difference in actual yield estimated in the field experiments and the yield the cultivar would give when it had the calculated optimal tolerance. This is done as follows. We calculate the expectation of the difference in actual yield in the case the cultivar would have the optimal tolerance level, $Y_{A,\,opt}$, and the case where the cultivar has the field-estimated tolerance level, $Y_{A,\,actual}$. Using Equation 2 we find

$$Y_{A,opt} - Y_{A,actual} = Y_F \mathrm{HAD}_{loss} \left(\alpha_{actual} - \alpha_{opt}\right). \tag{5}$$

where α_{actual} and α_{opt} are the field-estimated tolerance and the optimal tolerance, respectively. The expected value is calculated from

$$E\left(Y_{A,opt} - Y_{A,actual}\right) = \int_0^{\infty} P\left(\mathrm{HAD}_{loss}\right) Y_F \mathrm{HAD}_{loss} \left(\alpha_{actual} - \alpha_{opt}\right) d\mathrm{HAD}_{loss}. \tag{6}$$

which, using the fact that the HAD_{loss} distribution is exponential and expressing it as a percentage relative to the fully protected yield, we find

$$E\left(\frac{Y_{A,opt} - Y_{A,actual}}{Y_F}\right) 100 = 100 \left(\alpha_{actual} - \alpha_{opt}\right) E\left(\mathrm{HAD}_{loss}\right). \tag{7}$$

where $E(\mathrm{HAD}_{loss})$ is the mean HAD_{loss} value. This percentage difference in actual yield quantifies the extent to which breeding for tolerance is a worthwhile breeding target even under a fungicide treatment regime.

3 | RESULTS

Figure 2, top left panel, shows that the function $Y_F = a\ln^2(x) + b\ln(x) + c$, with parameter values $a = -1.725$, $b = -12.34$, and $c = -11.326$, gives a good description of the outer envelope of the data. Cultivars with combinations of tolerance and fully protected yield inside the envelope are possible outcomes of a breeding programme.

Our breeding goal is to maximize actual yield, and Figure 2 will tell us what combination of tolerance and fully protected yield maximize actual yield. The contour lines for equal actual yield, Equation 3, are plotted together with the enveloping line in the other panels of Figure 2. In the top right panel the HAD-loss equals zero, meaning there is no disease. We see, for example, that breeding for an actual yield of 9 t/ha is possible for tolerances between 0.012 and >0.06, or it is possible to breed for an actual yield of 10 t/ha, with a tolerance between 0.015 and 0.06. Because we aim for maximum actual yield, the $Y_A = 10$ is a better aim than $Y_A = 9$. For an actual yield of 10.74 t/ha the line just touches the tip of the envelope. At this point the fully protected yield equals 10.74 t/ha and the matching tolerance is 0.028. From this we conclude that if disease was absent or could be controlled completely (i.e., HAD-loss equals zero), the target is to breed only for the maximum fully protected yield.

For a HAD-loss of 10 (Figure 2 bottom left panel) we can follow the same reasoning, concluding that the maximum actual yield we can breed for is 8.57, where the hatched line just touches the envelope. For this HAD-loss the yield and tolerance that maximizes the actual yield is 10.1 t/ha and 0.015, respectively. For a HAD-loss of 10 we do not breed for the maximum possible fully protected yield but accept a slightly smaller yield potential in order to gain a higher level of tolerance. In the presence of disease, this results in the largest actual yield.

The three panels with actual yield contour lines show that the larger the HAD-loss, that is, the higher the disease severity, the more we need to target at breeding for tolerance and compromise on the achievable yield. In each panel the optimal tolerance and fully protected yield is marked with a dot and a number. These dots and numbers reappear in Figure 3.

Figure 3 shows that the tolerance that maximizes actual yield increases with increasing HAD-loss, as we concluded from Figure 2. The tolerance seems to level off at approximately 0.07 for larger values of the HAD-loss. The right-hand panel of the figure shows the difference between the fully protected yield that, together with the appropriate tolerance, produces the maximum actual yield, and the associated actual yield. The dashed line is the actual yield for a cultivar that was bred to maximize actual yield in the absence of disease. Above a HAD-loss of 5, the realized yield at optimal tolerance and the actual yield for a cultivar bred to maximize fully protected yield in disease-free situations start to deviate. This shows that breeding for the optimal level of tolerance starts to pay off for HAD-losses above 5.

As discussed earlier, there are year-to-year variations in epidemic severity and thus year-to-year variations in HAD-loss. Figure 4 shows HAD-loss distributions for untreated fields and for fields receiving a fungicide treatment programme. Some of the estimated HAD-losses are smaller than zero, probably due to measurement errors at sites and seasons with negligible disease. We have omitted these results from the further analysis. Exponential distributions fitted well to the data ($R^2 = 0.97$ for the untreated and 0.99 for the treated case). The bottom left panel shows the dependence of the mean HAD-loss on the resistance rating of the cultivar. As expected, the mean HAD-loss decreases with increasing disease resistance rating.

The long-term mean tolerance that maximizes actual yield, Equation 4, is plotted in Figure 5 as a function of the cultivar resistance rating. These tolerance levels are the tolerance that, taking account of year-to-year variation in HAD-loss, maximizes actual yield. These tolerance levels thus are the breeding target. In the left-hand panel of Figure 5, the tolerance breeding target is plotted for both the untreated fields and fields receiving a fungicide treatment programme. In the right-hand panel the left hand panel is plotted again, but on a different y axis, enabling us to plot the tolerance of the commercially available cultivars that were assessed in the experiments. From the figure we see that the tolerance of some commercially available cultivars agrees closely with the tolerance that results in the maximum mean actual yield. These are Avalon, Cadenza, and

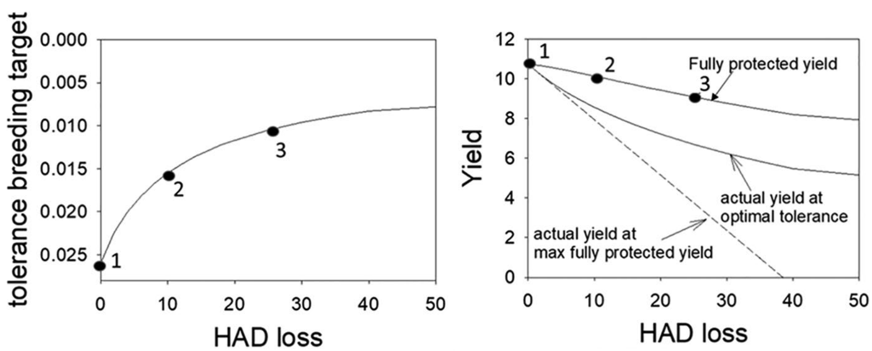

FIGURE 3 Left: The tolerance breeding target that maximizes actual yield as a function of HAD-loss due to disease. The dots with numbers represent the same cases/breeding targets as in Figure 2. Right: Yield as function of HAD-loss. Top line is the fully protected yield that forms the breeding target maximizing actual yield. The dots and numbers represent the same cases/breeding targets as in Figure 2. Lower drawn line is the actual yield as a function of HAD-loss when the cultivar is bred for the optimal combination of yield and tolerance. The lower dashed line is the actual yield for a cultivar that is bred to yield maximally under no disease intensity (Figure 2 top right)

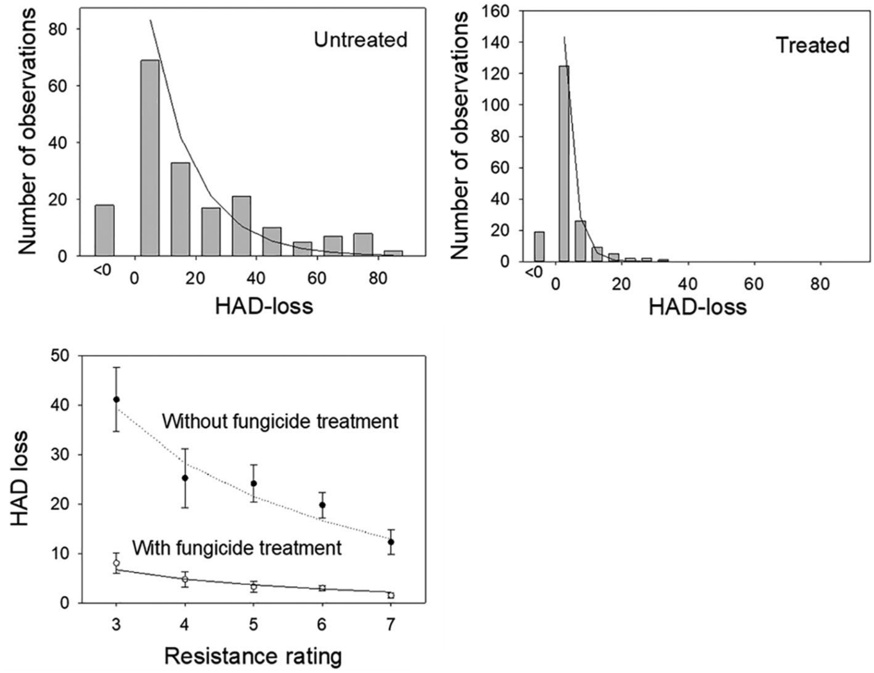

FIGURE 4 The number of years where a given HAD-loss is observed. Left: Crops not receiving a fungicide treatment programme. Right: Crops receiving a fully effective fungicide treatment. Each case has a small number of negative HAD-loss values, these are omitted in the further calculations. Bottom left: Mean HAD-loss over all observations in the top panels as a function of resistance rating. Hashed line, crops that do not receive any fungicide treatments; solid line, crops that receive a fully effective fungicide treatment

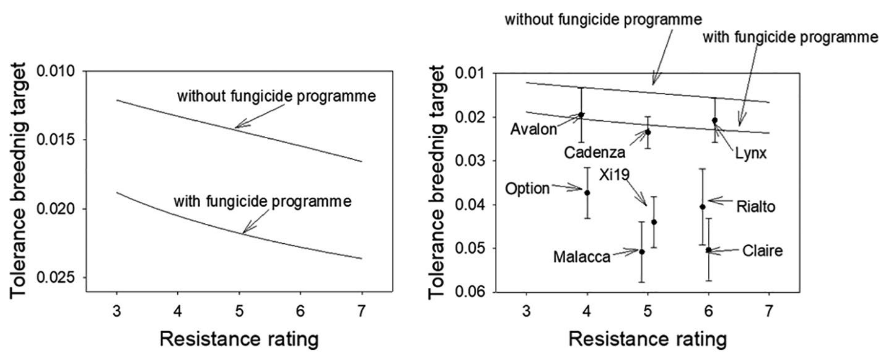

FIGURE 5 Breeding target for tolerance to disease when the year to year variation in HAD-loss (Figure 4) is taken into account, as a function of the cultivar's resistance rating. Both panels show the same lines, only the *y* axis is scaled differently. This is done so that in the right-hand panel the field estimated tolerance of commercially available cultivars can be plotted

TABLE 3 Cultivars and their resistance rating and tolerance

Cultivar	Resistance rating[a]	Optimal tolerance[b]	Estimated tolerance[c]	Yield loss due to lack of tolerance (%)[d]
Avalon	4	0.0205	0.0195	0.4
Cadenza	5	0.0218	0.0235	0.6
Lynx	6	0.0228	0.0207	0.6
Claire	6	0.0228	0.0503	8.3
Malacca	5	0.0218	0.0508	8.1
Option	4	0.0205	0.0373	7.6
Rialto	6	0.0228	0.0405	5.4
Xi19	5	0.0218	0.0440	7.6

[a]The resistance rating as given in the Recommended List (Anonymous, 2021).

[b]The optimal tolerance as calculated using the model developed in this paper.

[c]The field estimate of the tolerance of the cultivar.

[d]The percentage yield loss due to the difference between the optimal and the actual level of tolerance.

Lynx. The cultivars Option, Xi19, Rialto, Claire, and Malacca have inadequate tolerance to ensure the maximum mean actual yield.

Finally, in Table 3, the percentage yield difference is shown for all the cultivars compared to a cultivar that would have had the optimal tolerance. As expected from Figure 5, for Avalon, Cadenza, and Lynx the difference is small. For the other five cultivars the yield loss caused by the deviation from optimal tolerance varies from 5.4% to 8.3%.

4 | DISCUSSION

The CIMMYT spring wheat Line 14 was crossed with the UK winter wheat cultivar Rialto to generate a DH population. The Line 14 advanced line contains the dominant spring wheat *Vrn-A1* allele for vernalization response on chromosome 5A, whereas the winter wheat Rialto contains the recessive *vrn-A1* allele; similarly Line 14 contains the dominant *Ppd-D1a* allele for photoperiod insensitivity on chromosome 2D, whereas Rialto contains the recessive *Ppd-D1b* allele for photoperiod sensitivity. The progeny thus segregated for winter/spring vernalization and photoperiod sensitivity/insensitivity characteristics. However, in the present experiments only lines exhibiting high vernalization requirement and photoperiod sensitivity were used (i.e., winter types) so there would be no wide variation in phenology and anthesis dates in the Line 14 × Rialto DH population. The Cadenza × Lynx and Xi19 × SHW populations will have been segregating for winter/spring *Vrn-A1* but in each case both parents were photoperiod-sensitive, so from mid-October or later sowings there would be no wide variation in anthesis dates as all lines will still have been photoperiod-sensitive, that is, floral initiation, switch from leaf to spikelet primordia initiation at the apex, is under the double lock of vernalization and photoperiod control, so even if there are differences in the timing of the vernalization requirement being satisfied these will have been overridden by the photoperiod sensitivity maintaining similar flowering times in the DH lines.

Some of the lines were omitted as described in section 2. By doing so, highly resistant lines were omitted, as resistance is not a topic of study and tolerance could not be quantified accurately on such lines. Moreover, very tall, very low yielding, and out of season flowering, and thus commercially irrelevant lines, were omitted. The fungicide programme used in the experiments was carefully chosen to avoid giving the protected plots an additional advantage over the untreated control plots via possible beneficial physiological effects. Nontarget diseases such as mildew, rusts, and eyespot were controlled in the experiments by applying the fungicides proquinazid, cyflufenamid, pyraclostrobin, and cyprodinil. The strobilurin (QoI) fungicides have been widely reported to have direct effects on plant physiology that may lead to enhanced yield in both the presence and absence of disease challenge. Mechanisms responsible include decreased respiration, increased photosynthetic rate, effects on nitrogen uptake, increased tolerance to stress, reduced ethylene production, and delayed leaf senescence, which is often termed the "greening effect" (Amaro et al., 2020; Beck et al., 2002; Bertelsen et al., 2001; Grossmann et al., 1999; Ruske et al., 2003). However, these fungicides were applied to all plots so any beneficial physiological effects would have occurred equally across the whole experiment.

The protected plots received azole fungicides (epoxiconazole and metconazole), which are not reported to enhance yield or delay senescence through direct physiological effects on the plant, but rather through robust control of visible disease symptoms, which in turn results in prolonged green leaf area and higher yields.

The analysis of breeding for tolerance quantified the extent to which disease tolerance is a relevant breeding target when the breeding goal is to develop cultivars with maximum actual yields. Even when an effective fungicide treatment programme is applied, some level of tolerance can increase the mean actual yield. For existing cultivars, the actual yield gain that could be obtained was estimated to be between 3.4% and 8.3%. Gains may also be obtainable from tolerance to other foliar pathogens that cause damage predominantly through loss of HAD.

The findings have implications for the methods used to assess the value of new cultivars and recommend their use to growers. Field experiments for the UK Recommended List system for cereals (Anonymous, 2021) use fungicide programmes that are more intensive than those used in commercial practice. This creates competition between breeders for cultivars with the highest treated yield under intensive inputs. Our analysis suggests that creating competition for the highest achievable yield would be more productive.

The HAD-loss distribution used to characterize the year-to-year variation in HAD-loss was based on data gathered in field experiments where fungicide applications were generally well timed. In farm fields the timeliness of fungicide treatments can be affected by the large area that needs to be treated and scarcity of good weather conditions for spraying (Anonymous, 2009), so it is likely that HAD-losses occur in practice that are larger than those in well-controlled experiments. The estimates of the yield losses of the eight commercial cultivars, caused by lack of tolerance, may therefore be underestimates. Hence, the optimal tolerance that maximizes actual yields may be higher than our calculations show.

Even when tolerance is optimized and in balance with fully protected yield, there is a difference between the fully protected yield of a cultivar and the actual yield. This yield gap cannot be reduced by agronomic measures because the yield gap is caused by the trade-off between tolerance and fully protected yield. This trade-off may be caused by random chance of genetic linkage or, more likely, by pleiotropic effects. For example, van den Berg et al. (2017), in a model study, and Foulkes et al. (2006), in a field study, both found that tolerance increases with decreasing number of grains per ear and number of grains per square metre of ground. Decreasing grains per ear increases source availability in relation to grain sink size. A lower number of grains per ear is likely to decrease yield potential, suggesting that genes that control yield potential are also affecting tolerance. Minimizing such trade-offs depends on identifying traits where the effects on yield and tolerance are not negatively associated.

The experiments on which the analysis was based used DH mapping populations derived from crosses of elite cultivars. These experiments resulted in the combinations of tolerance and fully protected yield available to breeding programmes in the progeny from which future cultivars could be selected. The possible breeding space is changing constantly—the varieties used as the parents in the crosses are already superseded by better cultivars. Further improvements in actual yield require the upper boundary of the breeding envelope of tolerance by fully protected yield to be shifted. Greater emphasis on selection for tolerance, across generations of a breeding programme, would change the boundary. Initiatives to increase access to diverse germplasm (Moore, 2015) and new techniques (Juliana et al., 2020; van de Wiel et al., 2017) in breeding programmes should increase the scope for gains in actual yield.

ACKNOWLEDGEMENTS

Funding of the experimental work by the Department for Environment, Food and Rural Affairs of the United Kingdom is gratefully acknowledged. Rothamsted Research receives support from the Biotechnology and Biological Sciences Research Council (BBSRC) of the United Kingdom. Thanks are due to colleagues in ADAS and Teagasc for their help in conducting the field experiments.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: van den Bosch, F., Smith, J., Wright, P., Milne, A., van den Berg, F., Kock-Appelgren, P., et al. (2021) Maximizing realized yield by breeding for disease tolerance: A case study for Septoria tritici blotch. *Plant Pathology*, 00, 1–9. Available from: https://doi.org/10.1111/ppa.13509