# Achievements in breeding cereals with durable disease resistance in Northwest Europe

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## 1 Progress in breeding for effective, durable resistance

Resistant varieties make an increasingly important contribution to control of diseases and pests of wheat, barley and oats in northwest Europe. Resistance is increasingly durable and the era of 'boom-and-bust', in which new resistance genes were rapidly rendered ineffective by the emergence of virulent pathogens, is for the most part long gone. In some cases, resistance is now so effective, widespread and durable that the diseases themselves have become much less significant, while a growing proportion of varieties are

not very susceptible to any of the most important diseases. The 'arms race' between breeders and pathogens is not yet over, but we are increasingly in an era when most disease resistance is stable and further advances can be foreseen.

As cereal breeding in this region is done almost entirely by the private sector, breeding for resistance cannot be done in isolation; rather, to produce varieties which are popular in a highly competitive market, breeders have combined durable resistance to multiple diseases and pests with the many other traits required by farmers and end-users which contribute to high yield, marketable grain quality and desirable agronomic properties. In the chapter, I describe the achievements of the cereal breeding industry in northwest Europe in developing commercially successful varieties with durable resistance and reflect upon the reasons for this success.

## 1.1 Cereal production in Northwest Europe

In northwest Europe, I include the United Kingdom (UK), Ireland, Scandinavia, the Benelux countries, France, Germany, Switzerland and Austria. This is a region in which arable farming is intensive with higher use of fertiliser and pesticides than in most other cereal-growing areas and in which crop yields are correspondingly high. The drive to produce high yields of cereals poses a significant challenge for disease control, including breeding for resistance, because many fungal diseases are much more severe when greater amounts of nitrogen fertiliser are supplied.

Wheat and barley are the main cereals in this region with the three highest producers of both crops being France, Germany and the UK (Table 1). The three Scandinavian countries, Denmark, Norway and Sweden, together rank fourth for both species, with a total not far behind the UK. Among these countries, the highest yields of wheat are in the UK while France, Germany and the UK have similar average yields of barley. The highest yields of all are, in fact, in Ireland, with 9.4 t ha$^{-1}$ wheat and 8.2 t ha$^{-1}$ barley. Rye, triticale and oats are minor crops in northwest Europe as a whole but are locally important. The majority of rye is grown in northeast Germany while most triticale is produced in Germany and France, often on marginal land. Oats is an important crop in northern areas including the UK and Scandinavia; again, the highest yields of all are in Ireland with 8.1 t ha$^{-1}$.

Winter wheat, sown in early autumn, is much more important than spring wheat, sown in late winter in almost all areas of northwest Europe. In both barley and oats, winter and spring crops are equally important. In the UK, in 2018 and 2019, there was an average of 1.8 million hectares of wheat, almost all of it winter wheat, 1.2 million hectares of barley with just over 60% being spring barley, and 180 000 hectares of oats (DEFRA, 2020).

**Table 1** Production areas and grain yields per unit area of small-grain cereals in northwest Europe. Data are from 2019.

| Crop[a] | Growing area in northwest Europe in 2019 (Mha) | | | | | |
|---|---|---|---|---|---|---|
| | Total | France | Germany | UK | Scandinavia[b] | Others[c] |
| Wheat | 12.07 | 5.24 | 3.12 | 1.82 | 1.12 | 0.77 |
| Barley | 6.25 | 1.94 | 1.71 | 1.16 | 1.00 | 0.43 |
| Rye | 0.93 | 0.03 | 0.64 | 0.03 | 0.19 | 0.05 |
| Triticale | 0.79 | 0.31 | 0.36 | 0.01 | 0.04 | 0.08 |
| Oats | 0.69 | 0.09 | 0.13 | 0.18 | 0.25 | 0.05 |
| | Mean yield in 2019 (t ha$^{-1}$) | | | | | |
| Wheat | 7.8 | 7.7 | 7.4 | 8.9 | 7.6 | 7.6 |
| Barley | 6.7 | 7.0 | 6.8 | 6.9 | 5.7 | 7.4 |
| Rye | 5.2 | 4.7 | 5.1 | 2.4 | 6.1 | 4.6 |
| Triticale | 5.8 | 5.4 | 6.1 | 4.5 | 6.3 | 5.6 |
| Oats | 5.0 | 4.6 | 4.1 | 5.9 | 4.7 | 6.0 |

[a] Crop production data from FAOSTAT (http://www.fao.org/faostat).
[b] Denmark, Norway and Sweden.
[c] Austria, Belgium, Republic of Ireland, Luxembourg, The Netherlands and Switzerland.

# 2 Sources of information about breeding for resistance

Cereal breeding in northwest Europe is done largely by companies rather than universities or public-sector research institutes. Although the leading breeders have diverse corporate structures, an important feature they share is that most information about their activities is confidential. Even so, it is possible to infer many of the industry's priorities from the performance of the varieties they produce. Inevitably some of the information in this chapter is personal knowledge, often gleaned from conversations with breeders.

Additional information about breeding for resistance can be found in academic research papers. These are usually most informative when the authors have worked closely with the industry and thus have a realistic view of the significance of diseases in crop production and are well informed about plant breeders' requirements.

## 2.1 The AHDB Recommended List

In this chapter, I focus largely on the United Kingdom, partly because it is the country with which I am most familiar but also because the UK's Recommended List (RL), published annually, is a valuable source of long-running, comparative information about cereal varieties. It evaluates varieties for traits which are important to farmers and end-users, including disease and pest resistance, and

is thus an important guide to breeders in prioritising the traits which most need to be advanced.

The RL was issued by the National Institute of Agricultural Botany from 1948 to 2001 and has been produced by the Agriculture and Horticulture Development Board (AHDB) since 2002. As AHDB is a levy body, the RL is largely funded by farmers with significant contributions in kind by breeders and other relevant industries. I make frequent references to the RL in this chapter, which can be found at https://ahdb.org.uk/rl for the current year and at https://ahdb.org.uk/rlarchive for 2004 onwards. Note the dating system used for the RL; from 2004 onwards, the RL for 2021/22, for example, recommended winter varieties for sowing in 2021 and spring varieties to be sown in 2022. Until 2003, the RL was published as a printed booklet with a different dating system. The RL for 2003, for example, recommends winter varieties to sow in 2003 and spring varieties for 2004. Other countries in northwest Europe operate systems similar to the UK's RL, although the details vary considerably. Priorities for breeders in the UK are generally similar to those elsewhere in the region because most of the leading companies are multinationals, with subsidiaries or affiliates across the continent. Differences in emphasis in different countries largely reflect the local significance of various diseases.

## 3 Release and recommendation of cereal varieties

### 3.1 Plant breeder's rights

The desire for confidentiality stems from the system of protecting intellectual property in cereal varieties in Europe. This is governed by Plant Breeder's Rights (PBR), also known as Plant Variety Rights, not by patents. PBR originated with the UPOV Convention (*Union Internationale pour la Protection des Obtentions Végétales*) in 1961 and were implemented in the UK by the Plant Varieties and Seeds Act 1964, amended by the Plant Varieties Act 1997 (DEFRA, 2011). In the European Union (EU), the corresponding legislation is a set of 12 Directives which regulate plant reproductive material (European Council, 2020).

An important advantage of this system of intellectual property is that once a variety has been granted PBR, the company that owns the PBR has the right to market the variety and to earn royalties from seed sales, but any other company is free to use it as a parental line in its own breeding programme. This enables advances made by one company to be spread widely throughout the industry, accelerating the spread of new germplasm for the benefit of growers and ultimately consumers. This has been highly beneficial in breeding cereals for resistance to pests and diseases.

## 3.2 National List and Recommended List trials

Release of a new cereal variety in the UK is a two-step process. The first is National List (NL) testing, in which the variety is trialled over two years for distinctness, uniformity and stability (DUS) and value for cultivation and use (VCU), including resistance to important pests and diseases. A variety which passes NL trials can be awarded PBR. In the EU, varieties with PBR can be entered on the Common Catalogue of varieties approved for sale in all member countries.

It is not obligatory for new varieties to be entered into RL trials, which are more extensive and detailed than NL trials, but in practice, the RL is an important marketing tool. The RL is compiled by the Wheat Crop Committee and the Barley, Oats and Other Cereals Crop Committee of AHDB. Varieties may be provisionally recommended if they are successful in the first year of RL trials and fully recommended after a further two years of RL trials, making five years of official trials in total for the NL and RL. The RL for a particular cropping year is based on trials in years up to and including the previous year, so the 2021/22 RL, which was released in January 2021, is based on trial results in farming years up to and including 2019/20.

## 3.3 Disease ratings

Disease resistances are rated on a scale from 1 to 9, where 1 is very susceptible and 9 is largely immune. The scale is logarithmic, so differences in disease severity between integer ratings are much greater at the bottom of the scale than at the top. This is because when a variety has poor resistance to a disease, it does not matter very much just how poor it is, whereas smaller differences between good and very good resistance may influence farmers' choice of varieties.

The calculation of disease ratings is explained here: https://ahdb.org.uk/rl -disease-ratings. Disease severity in RL trials is scored on a percent scale, using a visual disease assessment key to promote consistency of disease scores at different trial sites. The use of percent data is more precise than the scoring systems used in most cases by breeders (see Section 5.3). Disease scores are transformed to logarithms and means for varieties are calculated across sites and across several years, recognising that disease severity is inherently variable. Linear interpolation is then used to convert the means of log-transformed disease scores to a 1–9 scale, with a very low score corresponding to 9 and a very high score to 1.

A complication in interpreting RL disease ratings is that they require the use of established varieties as controls to fix points on the 1–9 scale, usually 3 (susceptible) and 7 or 8 (resistant). If a control variety is significantly more or less susceptible than expected, the ratings of the varieties on the RL may

change. This explains the drop of about 1 point in the mildew ratings of spring oat varieties in 2010 (Fig. 5a) because the variety used to fix the low end of the scale had been less diseased than expected in several trials. Rarely, a rating scale may be recalibrated to reflect changes in the importance of a disease, as was done for wheat yellow rust in the 2021/22 RL.

The traits scored in RL trials reflect the requirements of farmers and end-users. When considering a variety for recommendation, the Crop Committee balances several traits by their importance, according to a set of weightings which the Committee has agreed in advance (AHDB, 2020). Four categories of traits are assessed: yield in various situations, grain quality, agronomic properties such as height, maturity date and lodging (the tendency to fall over in wind and rain), and resistance to pests and diseases. AHDB's Crop Committees each include several farmers and agronomists in addition to breeders, specialists in end-use sectors, a grain trader and a plant pathologist. This ensures that the UK's RL system focusses on the requirements of farmers, not the opinions of academic experts.

A few diseases are especially significant for farmers, and thus, for breeding. In winter wheat, resistance to Septoria tritici blotch ('Septoria') is one of only three traits with very high importance on the RL while resistances to Rhynchosporium leaf blotch ('Rhynchosporium') and net blotch are the only traits with very high importance in winter barley grown for feed; in winter malting barley, they are outweighed, rather obviously, by malting quality. For comparison, it is essential for yield to exceed a target value but so long as it does so, yield is treated as a character of high importance in wheat, barley and oats, to be balanced with other traits (AHDB, 2020).

Some varieties are given a regional or specific recommendation if either the breeder or the Crop Committee believes they will be commercially successful only in part of the UK or only for a specific purpose. This can include an unusual resistance to a pest or disease. Wolverine winter wheat was included in the 2021/22 RL with a specific recommendation for resistance to Barley yellow dwarf virus although its yield was lower than most other recommended varieties in its quality class, Hard Group 4.

## 4 Demand for disease resistance in cereals

Breeders can only be commercially successful if they produce varieties which are improvements on those currently available. Disease resistance is never sufficient on its own; a successful variety must combine resistance with high yield (inevitably the most important requirement), marketable quality and appropriate agronomic properties (Summers and Brown, 2013).

## 4.1 Why do we need resistant varieties?

There is demand for disease-resistant cereal varieties in northwest Europe for at least five reasons. First, farmers need to make a profit by minimising the cost of inputs, including fungicides and insecticides. Varieties with at least moderate resistance to all pathogens usually need fewer pesticide applications. Second, the farming industry as a whole benefits from suppressing disease. By growing resistant varieties, a farmer avoids spreading pathogens to her neighbours' fields (no doubt hoping her neighbours are equally considerate!) Third, the EU and all countries in northwest Europe have a policy of reducing the use of pesticides, so farmers increasingly need resistant varieties to control diseases because fewer effective chemicals are available. Fourth, when crops are damaged by pests and diseases, the resources used to grow the fraction of the crop that has been lost are wasted. Disease control thus contributes to reducing greenhouse gas emissions from agriculture (Berry et al., 2010). Last, resistance to fungicides has evolved in several important cereal pathogens, especially powdery mildew and Septoria of wheat, and powdery mildew and Ramularia leaf spot ('Ramularia') of barley (FRAG-UK, 2020). Economic crop production now depends on having varieties with at least moderate resistance to those diseases.

## 4.2 Minimum standards

The most important outcome of resistance breeding is to avoid producing 'disease suckers': varieties which are so susceptible that they spread disease to other varieties nearby with otherwise acceptable resistance. To be included in the RL, a new variety must achieve at least the minimum standard for resistance to several diseases, so that growing it does not pose an unacceptable risk for other farmers locally (AHDB, 2020). In effect, the minimum standard is a level of susceptibility where acceptable disease control can be achieved with an effective spray programme, using currently available pesticides. This is 3 for most diseases of cereals but 4 for Septoria of wheat. There is currently no minimum standard for resistance to invertebrate pests or viruses. The minimum standard takes account of the availability of resistance in breeding programmes, the timescale for improving resistance and the likely durability of resistance. The evidence from diseases such as powdery mildew of winter wheat and spring oats, brown rust of winter barley and Septoria nodorum blotch ('nodorum') of wheat is that having moderate resistance in most varieties is an effective route to achieving disease control at the national level.
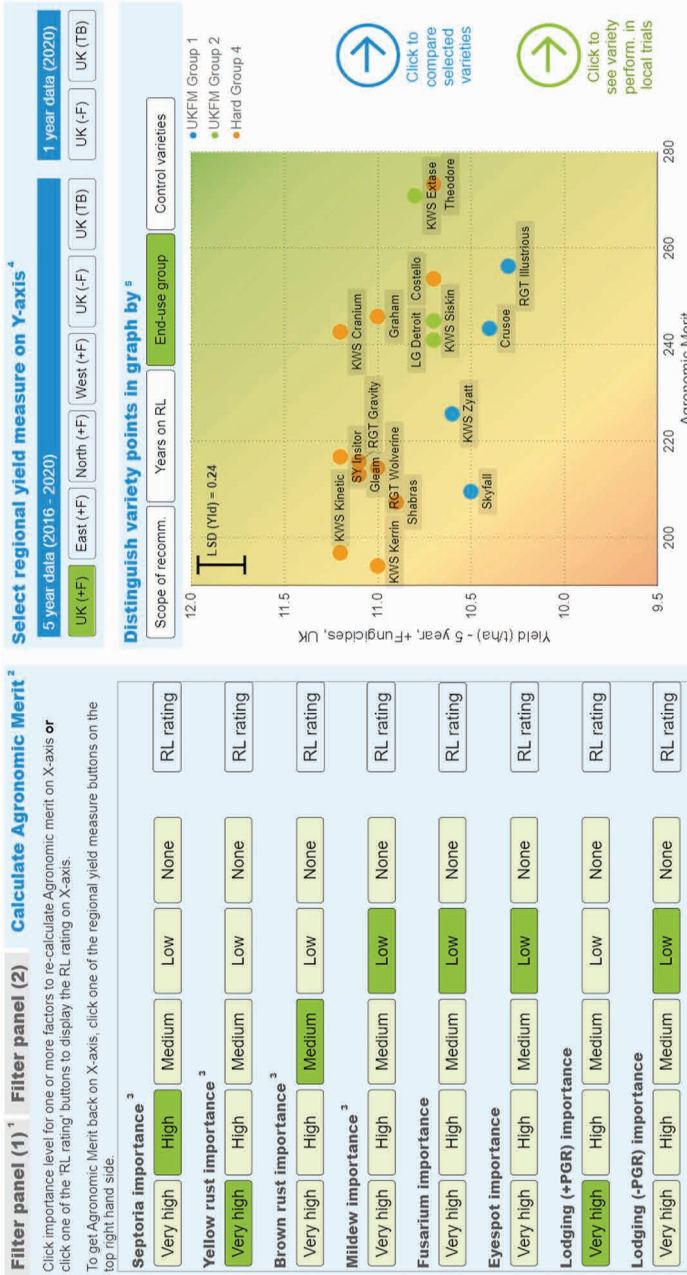
**Figure 1** A screenshot of the AHDB Variety Selection Tool for wheat, plotting yield in fungicide-treated trials as a measure of yield potential against agronomic merit, including disease resistance. The default weightings of the importance of different traits, as in the AHDB Crop Committee Handbook (AHDB, 2020), have been adjusted to suit the preferences of a hypothetical farmer in the east of England who wishes to grow a hard endosperm wheat, following another crop but not maize, with a plant growth regulator to reduce lodging. The choice of varieties is based on their average yields in trials across the whole of the UK. Reproduced by courtesy of the AHDB. © AHDB.

### 4.3 Variety Selection Tool: choosing a disease-resistant, high-yielding variety

The AHDB has recently introduced a Variety Selection Tool to help growers choose varieties that meet their requirements (https://ahdb.org.uk/vst). Most farmers wish to balance high yield against the risk of losses if diseases and lodging are not controlled, but some aim for higher yields while accepting greater risks while others wish to minimise inputs even if that means foregoing some yield. Moreover, farmers may have their own experience of the local significance of different diseases. The Tool is thus a flexible way for farmers to apply RL data to their own requirements.

The Variety Selection Tool plots yield in fungicide-treated trials as a measure of yield potential if diseases are well controlled, against agronomic merit calculated either from RL importance weightings or according to the farmer's own requirements. Figure 1 shows this for a hypothetical farmer in the east of England who wishes to grow hard endosperm wheat, following another crop but not maize, with a plant growth regulator (PGR) to reduce lodging. She believes yellow rust is more significant on her farm than Septoria while mildew, Fusarium and eyespot are negligible. She bases her choice on the full UK-wide dataset of trial yields. Among Hard Group 4 and Group 2 varieties, KWS Cranium has one of the highest yields with greater agronomic merit than its competitors, but if she wishes to minimise risk, she could consider Theodore or KWS Extase instead. Among Group 1 varieties, KWS Zyatt has the highest potential yield while RGT Illustrious has the greatest agronomic merit.

## 5 Breeding elite cereal varieties with resistance to multiple diseases

Plant breeding is a greatly accelerated form of evolution by natural selection (Brown, 2015). In nature, when there is *variation* in a phenotype, the phenotype is *inherited* and the variation affects *fitness*, natural selection follows as an inevitable consequence in a large population. Similarly, a successful plant breeding programme relies on identifying parental varieties with useful traits, an efficient system for crossing lines and developing progeny generations, and effective trialling to identify the best lines. In the words of the famous Soviet geneticist N.I. Vavilov, plant breeding is 'evolution directed by the will of man'.

### 5.1 Variation in many traits, including disease resistance

The need to balance many traits is reflected in the very large population sizes with which cereal breeders work. In winter wheat, a typical company produces many hundred thousand or even more than a million F2 plants each year,

which are reduced by stages to a few lines, often in single figures, submitted to NL trials each year. Of even this tiny subset of lines, only a minority become profitable as commercial varieties. These successful lines are exceptional because they are in the extreme of a distribution defined by many traits, controlled by rare combinations of genes. Part of the skill of a breeder is to balance the intensity of selection for all these features. This limits the potential for making rapid improvements in disease resistance in one generation or over very few generations because strong selection for a trait of moderate importance runs the risk of eliminating unusual combinations of genes which improve a more important trait (Summers and Brown, 2013). Nevertheless, the approach of making gradual improvements in the whole range of traits across successive generations has led to remarkable advances in durable resistance to most diseases of cereals in the UK and much of northwest Europe.

European breeders work with a range of sources of resistance. Crosses between leading local varieties have the highest chance of producing elite progeny lines with the traits required for current local conditions, including disease resistance, but do not introduce new genes. Crosses between varieties from different countries within northwest Europe can help to increase resistance above the level that can be achieved with local varieties alone. An example was the use of German wheat varieties to improve resistance to Septoria in the UK when it first became recognised as a major disease in the early 1980s (Arraiano and Brown, 2017). As the genetic distance between the source of resistance and the local population increases, however, the chance of introducing undesirable genes also increases. Arraiano and Brown (2017) found evidence that in the mid-1950s, when Septoria was barely known as a pathogen of wheat, genes increasing susceptibility to Septoria were inadvertently transferred into UK winter wheat from a German spring variety used as a source of increased yield and resistance to yellow rust. In more distant crosses, genes for resistance to mildew, rusts, eyespot and viruses have been introduced into wheat or barley from non-European landraces or wild grasses related to cultivated cereals. A challenge to using such exotic material routinely is that breeders must select lines which not only carry the desired resistance but also match the best varieties for yield, quality, agronomy and resistance to other diseases and pests. This requires topcrossing to the best current varieties for several generations to transfer the new resistance into a commercially competitive variety. The need to play catch-up limits the potential for breeders to use germplasm which has worthwhile resistance but is poorly adapted to local conditions; for example, it has restricted the use of resistance to Soil-borne cereal mosaic virus in European winter wheat (Summers and Brown, 2013).

It is challenging enough for breeders to decide how to balance the priority of many traits at any one time. Given that it takes nine years or more to bring a winter cereal variety from the initial cross to being fully recommended,

however, it is an even greater challenge to predict what farmers and consumers will require a decade after the cross is made. Some demands are quite easy to foresee – many breeders currently aim to produce varieties with yields which will be more robust in a less predictable climate – but others are harder, not least when they involve changes in pathogen genotypes or species. Until 2010, the wheat yellow rust fungus had limited genetic diversity in northern Europe. The huge increase in diversity from 2011 onwards (Hubbard et al., 2015; Hovmøller et al., 2016) came as a great surprise and has presented new challenges for resistance breeding.

Changes in policy for regulation of food production and the environment affect farmers' decisions, including their choice of crop varieties. A foreseeable development to which breeders have been able to respond to some extent has been the removal of several fungicides from the market by EU regulations, first announced in 2008 and implemented in stages since then (Punja, 2018). It was perhaps harder to predict the ban, announced in 2018, on applying neonicotinoid insecticides to crops which are not insect-pollinated (European Commission, n.d.). This has caused an urgent demand for resistance to insect pests and insect-borne viruses. Given the timescale on which cereal breeding operates, sudden changes in policy do not help breeders to produce the varieties that meet the requirements of farmers, consumers or society in general.

## 5.2 Pedigrees and breeding systems

A critical feature of successful breeding is to choose parents which have desirable values of important features but are genetically diverse. This generates transgressive segregation with phenotypes which exceed the range of the parental lines, so breeders can select progeny with new combinations of genes which improve the most important traits. This is critical to improving disease resistance and any other character. The choice of parents, therefore, tends to be treated as confidential. Although the NL requires breeders to state varieties' parentage, it has become common over the last 20 years for one or both parents to be named with serial numbers which mean nothing to people outside the breeding company. This creates a minor obstacle to studying the recent history of cereal breeding although high-throughput marker systems are now capable of substantially reconstructing pedigrees (Fradgley et al., 2019).

Each company has its own preferred system for incorporating sources of disease resistance into breeding programmes to combine resistance with yield, quality and agronomic properties. They also have their own preferences for methods of advancing lines through the generations. Important considerations are to ensure that varieties are genetically uniform, to carry out selection on multiple traits efficiently, and to test enough lines to have a high chance of finding the very few which are so exceptional that they may become profitable.

The pedigree system is capable of testing very many lines for different traits while advancing them by selfing through the generations (Koebner and Summers, 2003) but a considerable amount of 'pure stocks' work is needed to minimise segregation of traits even in advanced generations, so that candidate varieties pass DUS testing. Doubled-haploid methods produce uniform lines and allow exactly the same genotype to be tested for diverse traits, but do not have the capacity of the pedigree system to produce huge numbers of progeny from which rare, exceptional lines can be selected (Weyen, 2008). Single-seed descent (Snape and Riggs, 1975), including its modern development as 'speed breeding' (Watson et al., 2018), is a widely-used and effective compromise. Lines are advanced by selfing in conditions which produce small amounts of seed quickly, to produce F4 or sometimes F5 plants which are homozygous at most loci. This system can produce more lines each year than the doubled-haploid method and the lines themselves are more uniform than in the pedigree system.

### 5.3 Selecting for disease resistance

Methods of scoring vary according to the disease, the purpose of the trial and the breeder's preference. There is a rather pervasive view among academics that quantitative resistance is difficult to select (to pick one example from the many papers that make such a statement, see Pilet-Nayal et al., 2017) but that is incorrect for many diseases of cereals. It may or may not be difficult to quantify accurately the amount of disease on a plant, but that is not the purpose of scoring disease in breeding trials. The main goal is to remove lines which are too susceptible to be advanced to the next generation or to official trials. At one extreme, great progress in breeding wheat for mildew resistance was made in the 1970s and 1980s by scoring plants in early generations on a two-point scale: acceptable or too susceptible. At the other extreme, semi-quantitative scores like the RL's 1-9 scale are sometimes used, but ordinal scales with a few categories such as resistant, intermediate and susceptible (sometimes with very resistant and very susceptible) are more common. Whatever the system, it must identify unacceptably susceptible varieties with some confidence and a breeder must be able to use it to score very many lines rapidly.

Most selection of resistance is based on field trialling and in the end, what really matters is varieties' performance on farms. The method which reflects farming practice most accurately is to choose sites where natural infection is predictably high so that more resistant and more susceptible varieties can be differentiated. A practical limitation is that this may require breeders to travel to several distant sites in early summer. For some diseases, infection is promoted by inoculation with the pathogen and for rusts, most breeders inoculate trials with pathogen races of particular interest. Field trials are supplemented by

laboratory and greenhouse tests for some diseases. DNA markers are used by all companies to select important genes (Koebner and Summers, 2003) while the use of genomic selection is increasing (Poland and Rutkoski, 2016).

The choice of trial site is crucial for field selection of disease resistance phenotypes. For some diseases, varieties' susceptibility at a single well-chosen site gives a reasonably good estimate of their likely performance on farms. RL disease trials are run at geographically diverse sites to observe varieties' susceptibility in a range of conditions in case there is significant genotype-by-environment interaction (GxE), and the RL rating is calculated from the mean score across sites. It is not usually economic for breeders to run multiple trials for any but the most important diseases. GxE effects arise from local variation in pathogen virulence, especially in rusts and mildew, or from physiological variation in the expression of resistance, which is especially troublesome in Ramularia leaf spot of barley (Havis et al., 2015; Hoheneder et al., 2021).

A limitation on field phenotyping is the time that breeders can afford to score disease trials. This requires knowledge of the symptoms and sometimes the ability to distinguish different diseases, so there is great pressure on specialists within breeding companies to score many trials in a short period of time. There has been increasing interest in using image analysis technology, often combined with artificial intelligence, for scoring diseases in disease nurseries ( e.g. Mi et al., 2020). This has the potential to increase the amount of disease data obtained at a lower cost.

# 6 Durable and non-durable resistance

Disease resistance which is durable is especially desirable. For farmers, the requirement is not so much for durable resistance over many years as for predictable resistance over a growing season. They do not want a previously resistant variety to become unexpectedly susceptible because this incurs costs of additional pesticide applications or substantial losses from a disease which cannot be controlled. For breeders, durable resistance protects their investment in germplasm. When a variety's resistance 'breaks down' because it has been overcome through the evolution of virulent pathogen genotypes, the breeding company may lose its investment not only in developing and marketing that variety but also other, related varieties with the same resistance gene.

## 6.1 Race-specific resistance

There are broadly two types of genetic system controlling disease resistance in cereals, but there is a great imbalance between how well they are understood scientifically and how useful they are in breeding. Almost all academic research focusses on major genes which have strong effects and are amenable

to genetic and molecular analysis. Many of these genes, described as race-specific genes, encode receptors which induce defences when they recognise the presence of specific avirulent pathogen genotypes. The simple fact that they are overcome by pathogen mutations means that race-specific resistance is rarely durable against any disease of any crop and diseases of cereals in northwest Europe are no exception. Nevertheless, most breeders in northwest Europe are willing to use new race-specific resistances but accept that they are likely to break down sooner rather than later when virulent pathogen genotypes emerge. The situation that should be avoided is when resistance breeding relies heavily on repeated introductions of new race-specific genes, as happened in mildew of spring barley for several decades (Wolfe, 1984; Brown, 1994, 2015).

Toxin receptor genes are similar to race-specific resistance genes in biological function but not in coevolution with the pathogen. Necrotrophic toxins produced by a range of non-biotrophic fungi induce disease (rather than defence) through their interaction with a specific receptor (Faris and Friesen, 2020). Although the evolutionary biology of these interactions is less well understood than in race-specific resistance, mutations in a pathogen toxin may prevent it from interacting with the host's receptor and thus reduce pathogen virulence. Hence, resistance based on the absence of toxin receptors may be durable.

The length of time a pathogen takes to overcome a race-specific resistance depends on its mode of dispersal (Brown and Hovmøller, 2002; Wingen et al., 2013). Broadly, virulent mutants of wind-borne pathogens, including rusts and powdery mildews, can spread very rapidly over large areas while soil-borne pathogens disperse much more slowly. In the latter case, single genes for resistance to the soil-borne Barley yellow mosaic virus have been overcome by the pathogen, but the rate of dispersal of resistance-breaking viruses has been so low that breeders have had time to introduce new resistance genes (Ordon et al., 2009).

There has been significant interest among researchers in 'pyramiding' race-specific resistances, combining several such genes. This can be effective, at least temporarily, if the target pathogen has evolved virulence to each gene separately but genotypes which overcome the combination of all the resistances do not yet exist. The effectiveness of this strategy depends substantially on the pathogen's mode of reproduction. When it is asexual, breeders can introduce new race-specific resistances sequentially, keeping ahead of changes in the pathogen population. When it is conducted rigorously, this can be a durable strategy for deploying inherently non-durable resistances. It depends on having good survey data on the frequencies of pathogen virulences and races (Bayles et al., 1997; https://ahdb.org.uk/ukcpvs). Gene pyramiding is much less effective against sexual pathogens, however, because recombinant virulent

genotypes can overcome the combination of race-specific resistances (Brown et al., 1993).

Unfortunately, while research on the molecular biology of resistance has accelerated, genetic analysis and mapping of resistance to most diseases of cereals in northwest Europe have all but stopped in the last 25 years. It is clear from varieties' performance that new race-specific resistances to rusts, mildew, Septoria and other diseases have been introduced into breeding programmes (Figs 3–6) but most genes have not been identified individually and have not been mapped. This makes it difficult to know whether varieties have the same resistance, how widespread a particular resistance is in breeding programmes, and if a resistant variety has a new gene or a new combination of existing genes.

## 6.2 Durable resistance: mostly quantitative, mostly polygenic and mostly race-non-specific

Much more important in European cereal breeding is resistance which is polygenic and quantitative, effective against all genotypes of a pathogen species, and controlled by dispersed genes with minor or sometimes moderate effects. This type of resistance has many descriptions which largely overlap. Here, I call it quantitative resistance; other common names are partial, background and minor gene resistance. It is sometimes called race-non-specific resistance because it is effective against all genotypes of a pathogen species. This lack of genotype-specificity means that quantitative resistance is usually durable. In quantitative trait locus (QTL) mapping, it is usual for the statistical analysis to identify some genes which control moderately large, significant fractions of quantitative resistance but not to account for a substantial fraction of genetic variation. Presumably, this unexplained resistance is controlled by genes with effects too small to be detected individually but one can infer that such minor genes must be present.

There is a striking contrast between the intense interest of academic scientists in race-specific resistance, which has limited value in breeding arable crops, and their comparative neglect of quantitative resistance, which has much greater practical significance but is less tractable for molecular biologists. This could be described as the Cappuccino Model of plant disease resistance: an appealing surface layer (major genes or the froth on the coffee) covering the much larger part that does the effective work (durable host defences or the body of the drink with caffeine). Despite its importance in breeding, the physiological basis of quantitative resistance is poorly understood but it may largely concern variation in downstream defence processes rather than pathogen recognition (Corwin and Kliebenstein, 2017). It is common for academic research papers to say that knowing more about the underlying mechanisms will help breeders

select for disease resistance. This may involve microscopy of infection, modelling epidemiological parameters of infection processes or gene analysis expression associated with resistance, depending on the researchers' preference. The important point, however, is the simple one that breeders have successfully increased durable resistance to several diseases of cereals without such knowledge of defence mechanisms and often with little information even about the genetics of resistance. Having said that, the increasing power and rapidly decreasing costs of 'omics' technologies give academics the opportunity to restore some balance to the study of plant disease resistance.

'There is no single model for the genetic or phenotypic basis of durable resistance' (Johnson, 1993) and there are some important exceptions to the conflation of race-specific resistance with major genes, and quantitative, race-non-specific resistance with minor genes. A small minority of major genes control host defence rather than pathogen recognition, much the best known being *mlo* in spring barley, which gives near-complete control of powdery mildew (Kusch and Panstruga, 2017). It is not only genetically tractable but it confers durable resistance and is thus of great interest to both academics and breeders. Conversely, while almost all well-studied race-specific recognition genes have large effects against avirulent pathogens, there is wide variation in the effectiveness of such genes. This is apparent in many cereal diseases, including Septoria tritici blotch of wheat, where *Stb6* and *Stb15* have stronger effects on avirulent fungal isolates than other *Stb* genes (Brown et al., 2015). In powdery mildew of barley, some race-specific genes which have been named and mapped confer incomplete resistance or a high incompatible infection type (Jørgensen, 1994). There are similar examples in all the cereal rusts. Cowger and Brown (2019) suggested that the somewhat misleading view that all race-specific resistances are highly effective arose because breeders have chosen to use genes with the strongest effects, and that this has been reinforced by academics choosing to study the same genes because they are the most tractable.

Reviewing the durability of durable resistance, Cowger and Brown (2019) concluded that the rate of pathogen evolution to virulence on race-specific resistances with minor or moderate effects is slow enough for breeders to keep up with changes in the pathogen population. In practical terms, therefore, minor genes with race-specific effects can be treated as durable over a decade or more.

Race-specific recognition genes with strong effects are epistatic to variation in minor-gene, quantitative resistance. In some diseases, most strikingly powdery mildew of spring barley in Europe from the 1950s to the 1980s, reliance on such major genes has masked variation in quantitative 'background' resistance or susceptibility. This has led to spectacular breakdowns of resistance, when virulent pathogen genotypes have overcome a major gene in a variety with

little background resistance. It is therefore unwise (and usually unprofitable) to rely excessively on major race-specific resistances.

By contrast, when used effectively, race-specific resistance and quantitative resistance can work together in breeding. A strong major gene can give a variety a high rating on the RL and thus a boost in the early stages of its commercial life. When that resistance breaks down, as is almost inevitable, high quantitative resistance means the disease can still be controlled and the variety can still be profitable (note the brown rust resistance of NFC Tipple spring barley in Fig. 4, the crown rust resistance of Mascani winter oats in Fig. 5 and the brown rust resistance of Gladiator winter wheat in Fig. 6). Genomic selection offers a solution to the long-standing problem of knowing when strong race-specific resistance is combined with high quantitative background resistance. The race-specific resistance gene can be identified by its effectiveness against diverse pathogen genotypes (or possibly by molecular sequence data) while genomic selection can predict the quantitative resistance that is likely to remain when the major gene has broken down (Poland and Rutkoski, 2016).

### 6.3 Standing on the shoulders of giants

It is important to appreciate that disease resistance is not achieved in a single step. As with yield and many other traits, progress in breeding for durable quantitative resistance has come from applying effective selection in diverse populations over several generations. Nor is breeding a matter of chance: it is a misleading caricature to say that breeders 'cross the best with the best and hope for the best' (e.g. Podevin et al., 2013 – again, citing just one of many papers that make such statement). Of course, the actual F2 genotypes present in a population have random reassortments of the parental genes, but the choice of parents, selection methods and breeding system allow continual advances to be achieved so long as population sizes are large enough for a few really outstanding lines to be identified and developed as commercial varieties, and to be used as the next generation of parents. A more accurate metaphor is that breeders build on their own past successes and those of their predecessors: 'standing on the shoulders of giants'.

## 7 Resistance to biotrophic fungal diseases

Cereal breeders in northwest Europe have been successful in producing varieties with resistance to multiple diseases. In winter wheat and winter barley, breeders in the UK have increasingly produced varieties which are not susceptible to any of the main foliar fungal pathogens. Currently, on the 2021/22 RL, more than 70% of varieties have ratings of 5 or higher for all these diseases.

In wheat, this reflects improvements in Septoria resistance in particular. In every year since the mid-1980s, the RL for both crops has included at least one variety with at least moderate resistance to all the main foliar diseases, indicated by a rating of 6 or higher (Fig. 2).
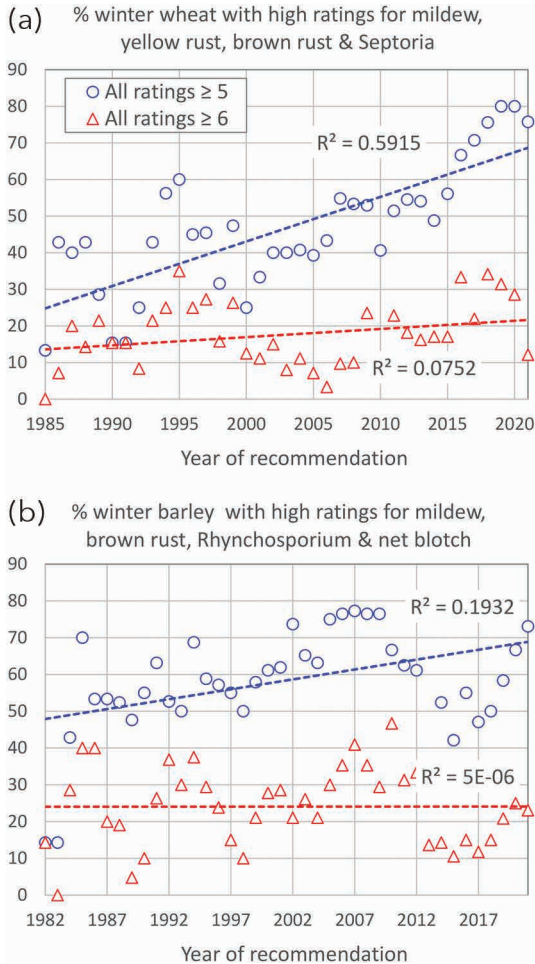


**Figure 2** The proportion of varieties of (a) winter wheat and (b) winter barley on the AHDB Recommended List which are rated as not susceptible to any of the main foliar diseases of each crop with a rating of 5 or higher (blue circles) or as resistant to all these diseases with a rating of 6 or higher (red triangles). The graphs start in the years when Septoria tritici blotch resistance was first rated in wheat (1985) and net blotch resistance was first rated in barley (1982). The large decrease in the number of winter wheat lines with broad-spectrum resistance between 2020/21 and 2021/22 is the result of a major recalibration of wheat yellow rust ratings, not a sudden drop in varieties' resistance.

## 7.1 Powdery mildew of spring barley: 'From the ashes of disaster...'

Powdery mildew, caused by the ascomycete fungus *Blumeria graminis*, is a potentially significant disease of barley, wheat and oats, especially on lighter land in cool, damp environments and in crops given large amounts of inorganic nitrogen fertiliser (https://ahdb.org.uk/powderymildew). It used to be one of the most important diseases of cereals in northwest Europe but has been well controlled by breeding, especially in spring barley, winter wheat and spring oats. Powdery mildew fungi are notorious for the speed with which they evolve insensitivity to fungicides so breeding for resistance has been essential for success in controlling this formerly troublesome disease. Mildew of the major small-grain cereal crops is caused by different forms (*formae speciales*) which are highly specialised on their host species, with *B. graminis* f.sp. *avenae* on oats, f.sp. *hordei* on barley and f.sp. *tritici* on wheat. There is similar specialisation in several rust fungi.

The history of mildew resistance in spring barley illustrates vividly the failures and successes of different breeding strategies. Until about 1990, mildew was much the most important disease of barley in northwest Europe and indeed one of the most significant of all crop diseases. The source of the problem was that breeders relied heavily on major recognition genes, especially in spring barley. There was a substantial research effort to discover new *Ml* genes for mildew resistance in several countries, notably Denmark and the former East Germany, and these genes were introduced into European varieties at an average rate of one every three years between the mid-1950s and the mid-1980s. They included several alleles of the complex *Mla* gene as well as other genes, while *Mlh* and *Mlra* were largely used in winter barley. Most of these genes were introduced from landraces, mainly from outside Europe, although *MlLa* came from a wild barley species, *Hordeum laevigatum* (Hilbers et al., 1992). Several genes were introgressed more than once from different sources (Jørgensen, 1994). All these genes were rapidly overcome by mutation of the pathogen to virulence, sometimes in as little as two years after the release of the first varieties carrying them. Breeders increasingly used combinations of these genes ('gene pyramiding') but they proved no more successful. During this period, mildew resistance in spring barley showed the characteristics of a textbook boom-and-bust process, over and over again (Wolfe, 1984; Brown, 1994; Fig. 1a in Brown, 2015). In short, major recognition genes have made no contribution to durable control of barley mildew.

## 7.2 Powdery mildew of spring barley: '...grow the roses of success'

The situation changed radically from the early 1980s onwards, for two reasons. First, mildew resistance in spring barley provides one of the very few instances

in plant pathology of a highly effective, durable, major gene. Recessive alleles of *Mlo* discovered as artificial mutations in the early 1940s confer almost complete resistance to mildew (Kusch and Panstruga, 2017). Initially, resistance was associated with more or less severe necrotic flecking which reduced yield. Although lines with less necrosis and higher yield could be selected, most mutant *mlo* alleles were unsuitable for use in breeding. Subsequently, a natural mildew-resistance allele in an Ethiopian landrace, *mlo11*, was introgressed successfully into spring barley breeding throughout northern Europe (Jørgensen, 1992). It is likely that *mlo11* is currently present in at least half of all varieties, covering at least half the spring barley growing area. In addition, a few varieties with an artificial mutation, *mlo9*, have been released.

Although the MLO protein is required for susceptibility of barley to powdery mildew, its biological function is not yet known. It is not a member of either of the main classes of recognition gene, the nucleotide-binding leucine-rich repeat protein (NLR) or receptor-like kinase (RLK) families. MLO is required for the fungus to successfully penetrate the plant's epidermal cells so it provides an example of resistance achieved by mutating a gene required for host susceptibility (Kusch and Panstruga, 2017). Pathogen genotypes with some adaptation to *mlo* resistance have been detected but the extent of adaptation has been minor and has not prevented *mlo* from being highly effective (Schwarzbach et al., 2002).

About the same time as *mlo11* and *mlo9* were first used on a large scale in the 1980s, interest also grew in selecting varieties with partial resistance to mildew, in the expectation that this would enable barley breeders to escape the endless treadmill of discovering, using and losing major recognition genes. Most current spring barley varieties which have a functional, mildew-susceptibility allele of *Mlo* have very high quantitative resistance. This advance may have been facilitated by fewer major race-specific genes being used, which has made it possible to detect variation in quantitative 'background' resistance. By one route or other, the importance of mildew on spring barley has been greatly diminished. It is given a weighting of high importance in the RL system because few fungicides effective against barley mildew are now available, so it is essential for this level of resistance to be maintained.

### 7.3 Powdery mildew of wheat, oats and winter barley

Breeding for resistance to powdery mildew of wheat (*B. graminis* f.sp. *tritici*) has been outstandingly successful in the UK and most other countries in northern Europe. Until the early 1980s, mildew was one of the most serious foliar diseases of wheat and it was still troublesome until the mid-1990s. Breeding for resistance has reduced its importance so much that it can be hard to find in crops in the dryer parts of the UK. Wheat mildew is now resistant to most

fungicides so, like barley mildew, it is important for this generally high level of resistance to be maintained.

Some major genes were used in breeding both winter and spring wheat for mildew resistance between the 1950s and the 1980s (Bennett, 1984). Since the mid-1980s, several other, unnamed race-specific resistances have entered UK wheat breeding programmes, whether introduced intentionally or otherwise, but they have not contributed significantly to long-term control of mildew, and there has been little investigation of their genetics. Some of these, such as the mildew resistance genes in the wheat varieties Shamrock and Robigus came from a large set of lines derived from *Triticum dicoccoides* in the Netherlands, which were first used by Dutch breeding companies and then more widely (Lange and Jochemsen, 1992). The same *dicoccoides* material has contributed genes for resistance to yellow rust, brown rust and Septoria but so far as I am aware, none of them have been durable.

Quantitative resistance has been much more important than major genes in breeding for mildew resistance. It has been achieved by phenotypic selection over many years despite very limited knowledge of genes controlling quantitative resistance. In the UK, where breeding for mildew resistance in winter wheat and spring oats has been especially successful, no single quantitative resistance gene has been identified in either crop. With only a few exceptions, breeding for quantitative resistance to mildew in winter wheat has become a 'virtuous circle' because most parental lines have at least moderate resistance, so it is easy to select progeny with similar resistance. Most current varieties have RL ratings of 6 or 7 and many varieties from the mid-1980s onwards have had a rating of 8. Only two varieties recommended in the last 40 years have had a rating of 3. This degree of durable resistance protects varieties against severe epidemics when a major gene breaks down, as in Robigus, which had a new, unidentified mildew resistance gene, and its daughter variety Glasgow (Fig. 1b in Brown, 2015). Most spring wheat is grown in the south and east of England where severe mildew epidemics are now almost unknown and all currently recommended varieties have moderate to high mildew resistance with ratings from 6 to 8. A challenge for breeders now is to find trial sites where mildew epidemics occur regularly so that selection for resistance can be conducted reliably.

As the resistance allele is recessive, natural *mlo* mildew resistance is unknown in hexaploid wheat because the functional, wild-type, mildew-susceptibility allele in one genome complements *mlo* mildew resistance mutations the other genomes. Several workers have mutated or inactivated all three *Mlo* genes in bread wheat to generate complete resistance to mildew (Wang et al., 2014; Acevedo-Garcia et al., 2017) and both genes in durum wheat (Ingvardsen et al., 2019). This is undoubtedly an impressive technical feat although its practical benefit is perhaps less clear, at least in northwest Europe.

Despite its prevalence in spring barley, *mlo* has not been used successfully in winter barley breeding despite several attempts to introduce it, which suggests there may be a more significant penalty of *mlo* mildew resistance in winter than spring cereals. Moreover, quantitative resistance to mildew in wheat, which is no longer a major disease in many areas, has been one of the leading success stories of plant breeding in northern Europe. This does not mean that multiple
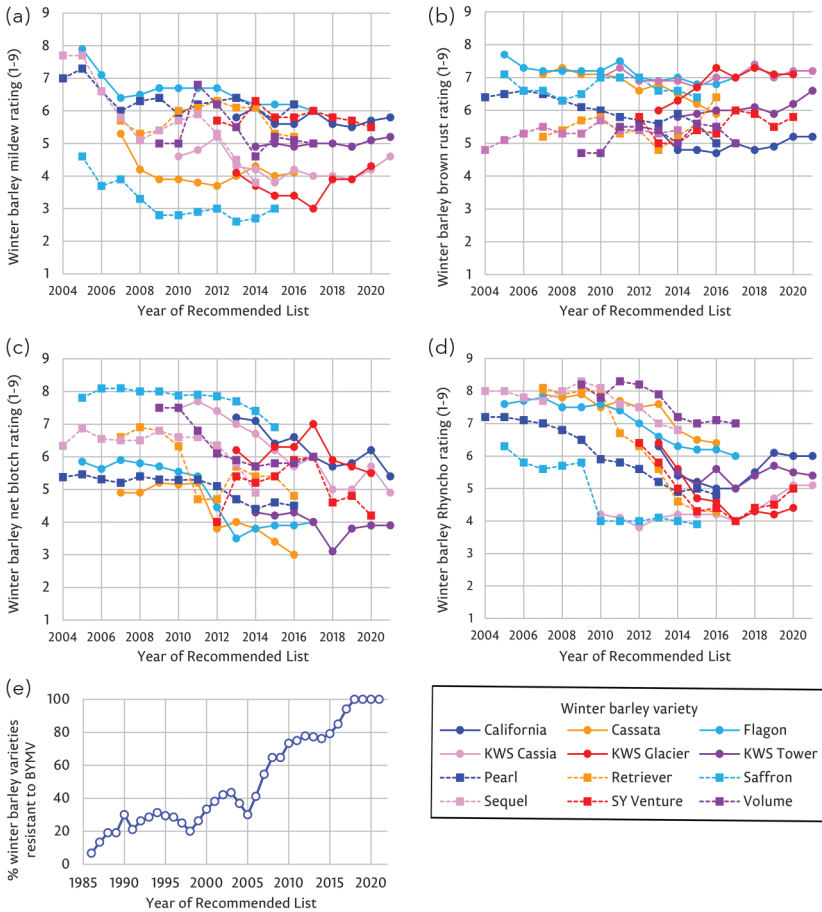


**Figure 3** Ratings of winter barley varieties on the AHDB Recommended List for resistance to (a) powdery mildew, (b) brown rust, (c) net blotch and (d) Rhynchosporium over the period that the RL has been produced in its present form from 2004/05 to 2021/22. Varieties which were on the RL for at least seven years during this time are included. (e) The proportion of winter barley varieties on the RL with resistance to Barley yellow mosaic virus from the introduction of Sonate, the first resistant variety. Resistance is presumably conferred by *rym4*.

knockouts of the wild-type *Mlo* gene may not be useful elsewhere in the world, possibly in spring wheat by analogy with the use of *mlo* in spring barley.

Mildew resistance in winter barley also relies on polygenic, quantitative resistance although not at successfully as in wheat (Fig. 3a). Current varieties have ratings between 4 and 7 with only LG Flynn having 3. While it may be
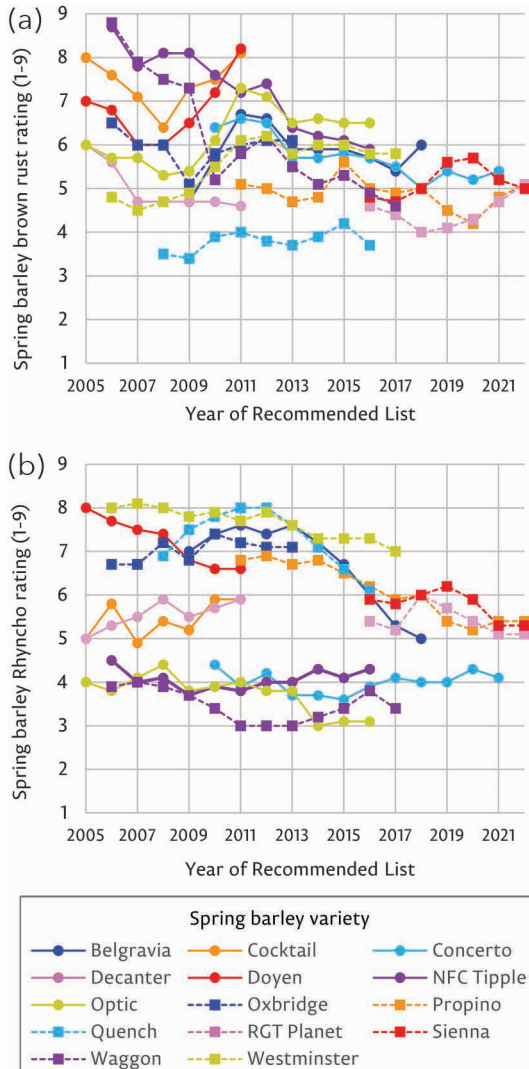


**Figure 4** Ratings of spring barley varieties on the AHDB Recommended List for resistance to (a) brown rust and (b) net blotch between the 2004/05 and 2021/22 RL. Varieties which were on the RL for at least seven years during this time are included.

desirable to increase the average level of mildew resistance, breeders currently focus on Rhynchosporium and net blotch. *mlo* incurs significant fitness penalties (reviewed by Brown and Rant, 2013; also see McGrann et al., 2014; Gruner et al., 2020; Jacott et al., 2020) so one can speculate that in winter barley, the costs of this resistance may outweigh its benefits.

Mildew resistance in oats has moderate importance and has depended almost entirely on quantitative resistance. This has been especially successful in spring oats (Fig. 5a), which are on a par with winter wheat, as most popular varieties have moderate to high quantitative, durable resistance. Mildew resistance has been weaker in winter oats (Fig. 5b).
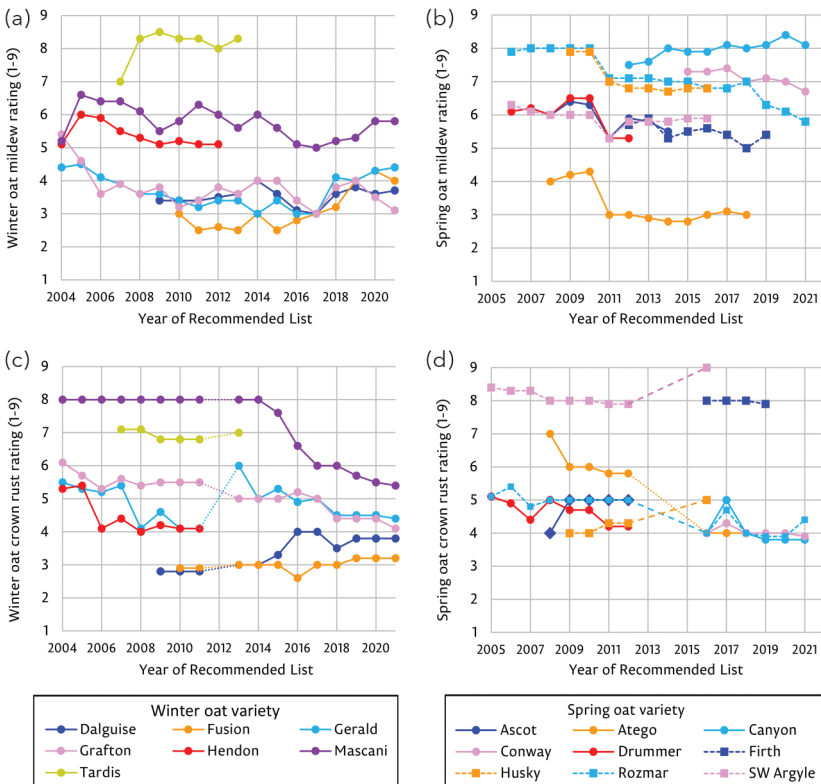


**Figure 5** Ratings of oat varieties on the AHDB Recommended list for the two main diseases between 2004/05 and 2021/22. (a) Resistance to powdery mildew of winter oats, (b) powdery mildew of spring oats, (c) crown rust of winter oats and (d) crown rust of spring oats. Varieties which were on the RL for at least seven years during this time are included. Low disease levels meant that crown rust ratings were not produced in 2012/13 for winter oats or in 2012/13, 2013/14 and 2014/15 for spring oats.

### 7.4 Yellow rust and brown rust of wheat: 'The times they are a-changing'

Wheat in northwest Europe is currently affected by two rust diseases: yellow rust, also known as stripe rust, caused by *Puccinia striiformis* f.sp. *tritici* (*Pst*), and brown or leaf rust (*Puccinia triticina*). Yellow rust was historically more severe in cooler northerly areas of Europe but recent changes in the climate and the pathogen population have increased its importance more widely. Brown rust continues to be the dominant rust disease in warmer, southerly areas within northwest Europe but climate change is leading to more severe epidemics further north.

Breeding for wheat yellow rust resistance has continued in England for nearly 120 years, longer than any other disease of cereals. It currently has high importance for variety recommendation. Although yellow rust can cause yield losses comparable to Septoria, it can be controlled by fungicides on varieties with moderate resistance. All breeders run nurseries to select yellow rust resistance, either exposed to natural infection or inoculated with specific *Pst* isolates. Eastern England from Cambridge to York is the prime hot-spot for wheat yellow rust in the UK and indeed Europe, and is thus a favoured location for breeders' trials.

The history of breeding wheat in northwest Europe for yellow rust resistance divides into two phases. Until 2010, the *Pst* population in this region was entirely asexual (Hovmøller et al., 2002). Major genes were widely used to control yellow rust, including *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr9*, *Yr17* and *Yr32* while *Yr7* and *Yr8* were regionally significant. Several other major gene resistances were used in important varieties but were not identified or mapped. In several countries, there have been surveys of the *Pst* population to monitor changes in pathogen virulence to major genes in current varieties. The UK Cereal Pathogen Virulence Survey has been run continuously since 1967, following the spectacular breakdown of yellow rust resistance in Rothwell Perdix (Johnson, 1992). Up to 2010, the clonal population of *Pst* evolved in a step-wise manner so pathogen survey data could indicate if new varieties were at risk of attack from the limited range of races of *Pst* in the current population (Bayles et al., 1997).

The situation changed dramatically in 2011 when a new population of *Pst* with much greater genetic diversity infected wheat crops throughout western Europe. It was later discovered that these genotypes originated in eastern Asia, where *Pst* is a sexual organism with *Berberis* species (barberry and mahonia) as alternate hosts (Hovmøller et al., 2016). The new fungal population rapidly overcame major resistances in Warrior and Torch, and there was great concern that much of the yellow rust resistance in existing European varieties could become ineffective. There were further significant changes in genetics and virulence of the *Pst* population in 2014 and 2016 but it is not known if the new genotypes were selected from the population which arrived shortly before 2011 or from fresh incursions. The geographic range over which yellow rust is significant has

expanded and the severity of yellow rust on established varieties has increased. This might have resulted from wider environmental adaptation among diverse *Pst* genotypes and from natural selection for greater aggressiveness (Pope de Vallavieille et al., 2018). Such adaptive variation has also been reported in *Pst* within France (Enjalbert et al., 2005). Although the new *Pst* population originates from a sexual population which has much greater capacity for telium production than the pre-2011 clonal races in northern Europe (Ali et al., 2010), there is as yet no evidence that it can reproduce sexually on *Berberis* in Europe.

Although the new *Pst* population overcame some major genes, perhaps the most remarkable feature of the new situation is that the quantitative resistance of many varieties continues to be effective while some varieties, notably Crusoe and Revelation, have very strong resistance which has been durable through the large genetic shifts in the *Pst* population in 2014 and 2016 (Fig. 1a in Cowger and Brown, 2019). In addition, Gladiator, which was on the RL until 2010, continues to be important as a source of durable resistance to yellow rust. Varieties with apparently durable resistance to yellow rust have also been identified in France, including Soissons and Scipion (Perronne et al., 2017). Evidently, durable resistance to the old clonal population was largely effective against the new, diverse *Pst* population. In retrospect, perhaps this should not have been surprising: if quantitative resistance does indeed largely involve downstream defences rather than pathogen recognition, it may be effective against all genotypes of a pathogen species and thus can control a new *Pst* genotype from East Asia just as well as an indigenous race from northwest Europe. The greater severity of epidemics caused by new, more aggressive genotypes of *Pst* means that recent advances in quantitative resistance to yellow rust (Fig. 1d in Cowger and Brown, 2019) need to be sustained.

An interesting feature of the new type of yellow rust is that some varieties have become more resistant during one or other of the three major recent changes in the *Pst* population, for example, JB Diego in 2011, KWS Santiago in 2014 and Viscount in 2016 (Fig. 1a in Cowger and Brown, 2019). Presumably, these varieties had recognition genes which were moderately effective against new *Pst* populations or there is some variation in the effectiveness of varieties' quantitative resistance to different fungal genotypes.

Breeding wheat for brown rust resistance has followed a similar pattern to yellow rust in the United Kingdom, with breeding for quantitative resistance punctuated by occasional breakdowns of major genes (Fig. 6). The average level of resistance to brown rust in the United Kingdom has not been as high as to yellow rust but it is a less important disease in most parts of the country. Almost all varieties on the 2021/22 RL have ratings between 5 and 8 except for Crusoe with 3 and LG Astronomer with 9; it is not known whether LG Astronomer has a major gene and thus may be at risk of breakdown or has outstanding quantitative resistance.
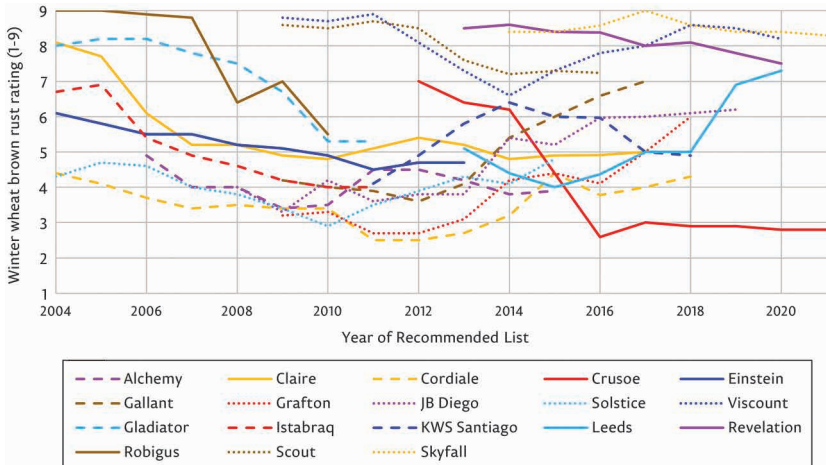
**Figure 6** Ratings of winter wheat varieties on the AHDB Recommended List for resistance to brown rust between 2004/05 and 2021/22. Varieties which were on the RL for at least eight years during this time are included, as well as Robigus as an example of a strong resistance 'breaking down' owing to the evolution of virulent pathogen genotypes.

Less is known about the European *P. triticina* population than about *Pst* but it is being studied in a project funded by the EU, RustWatch, from 2018 to 2022 (https://cordis.europa.eu/project/id/773311). It is striking that as with yellow rust, the brown rust resistance ratings of some wheat varieties have risen over time. There was a rapid rise in the rating of Leeds between 2018 and 2019 and more gradual increases in the ratings of KWS Santiago, Grafton, Gallant and Viscount over several years in the 2010s. One would not normally expect resistance ratings of widely-grown varieties to rise significantly during their commercial lifetime, so these changes suggest that there may have been incursions of new populations of *P. triticina* into northwest Europe with less virulence or lower aggressiveness to some varieties, just as in *Pst*.

Surveys of variation in rust virulence are as important now as they were in the era of the older, simpler *Pst* population (Bayles et al., 1997; https://ahdb .org.uk/ukcpvs). One of the most important activities of the UKCPVS is to make a representative selection of *Pst* and *P. triticina* isolates for breeders to use in rust trials. This selection is updated each year and trials with diverse, relevant isolates have made a critical contribution to breeding for durable resistance to both yellow rust and brown rust.

A challenge for releasing resistant varieties is that quantitative resistance is sometimes not strongly expressed in seedlings. It is understandable that farmers who have suffered at the hands of yellow rust epidemics on Torch, Warrior and other varieties and brown rust on Stigg or less dramatically Crusoe (Fig. 6) may not completely trust the assurances of agronomists that durable, adult-plant resistance

will protect their wheat fields. Hopefully, continuing success in advancing durable rust resistance will increase farmers' confidence in new varieties.

### 7.5 Brown rust of barley

The most important rust disease of barley in northwest Europe is brown rust (also known as leaf rust), caused by *Puccinia hordei*. Even so, it only has moderate importance for both winter and spring varieties on the UK's RL. Like yellow and brown rusts of wheat, it can be controlled quite easily with fungicides. Breeding winter barley for durable resistance to brown rust has been remarkably successful. Almost all recent varieties have had moderate to high quantitative resistance and ratings have been largely stable (Fig. 3b). The most significant exception was Valerie, which fell from 8.5 to 6.0 between the 2020/21 and 2021/22 RL. Quantitative resistance has not been as strong in spring barley as in winter barley in recent years, although varieties' ratings have been largely stable (Fig. 4a).

### 7.6 Yellow rust of barley

Where has all the yellow rust of barley gone? Until the 1980s, it was a significant disease although less so than yellow rust of wheat. It is still found occasionally in areas where wheat yellow rust is also important but at very low levels. It is an important disease of barley elsewhere in the world, while wheat yellow rust has become more significant than ever. Might this be an unheralded achievement of cereal breeding: the near-elimination of a formerly major disease by durable resistance?

### 7.7 Crown rust of oats

In contrast to mildew, popular winter oat varieties are slightly more resistant to crown rust (*Puccinia coronata*) on average than spring oats although most varieties are intermediate to moderately susceptible (Fig. 5c and d). Resistance is largely quantitative and durable. Mascani may have a major gene which broke down between 2014 and 2016 but it has been protected by moderate quantitative resistance. International research on crown rust resistance has largely focussed on major genes, and it is only recently that academics have paid significant attention to durable, quantitative resistance to crown rust, especially in Australia (Nazareno et al., 2018). This is surely an area for future development.

## 8 Resistance to non-biotrophic fungal diseases of wheat

In northwest Europe, the most significant diseases of wheat caused by non-biotrophic fungi are Septoria (*Zymoseptoria tritici*, formerly *Mycosphaerella*

*graminicola*), nodorum blotch (*Parastagonospora nodorum*), tan spot (*Pyrenophora tritici-repentis*), eyespot (*Oculimacula yallundae* and *Oculimacula acuformis*) and Fusarium head blight (*Fusarium graminearum*, *Fusarium culmorum* and other *Fusarium* species; Xu and Nicholson, 2009). Of these, Septoria is the most economically important disease of wheat in northwest Europe as in many other parts of the world.

## 8.1 Septoria tritici blotch

Septoria is most significant in regions with mild winters and warm, damp springs, including much of northwest Europe. Several factors have combined to make Septoria a disease of very high importance in winter wheat. First, climate change has reduced the number of nights with sub-zero temperatures in November and December, the critical period for establishment of Septoria epidemics by *Z. tritici* ascospores (Hunter et al., 1999). Second, *Z. tritici* is highly sensitive to sulphite in rainwater (Chandramohan and Shaw, 2013), which has declined as less coal has been burnt for power generation. Third, in the mid-1950s, before Septoria was even recognised as a disease of wheat in Europe, genes which increase susceptibility or reduce resistance to Septoria were inadvertently introduced in a breeding programme which subsequently fed into all wheat pedigrees in the UK (Arraiano and Brown 2017). Lastly, Septoria is the main target for fungicide applications on wheat and as a result, *Z. tritici* has become increasingly resistant to most fungicides (FRAG-UK, 2020). In the UK, Septoria is most severe in southwest England, where winters are mild and spring rainfall is plentiful. It is especially destructive in southeast Ireland, which is thus a favoured location for Septoria trials. Spring wheat is much less affected by Septoria because it avoids infection by ascospores in late autumn.

Breeding for Septoria resistance has relied almost completely on selection for quantitative resistance, which has been durable (Fig. 1d in Brown, 2015) . The average level of resistance has increased greatly in the UK over the last 35 years. In 1985, all fully recommended winter wheat varieties had ratings or 3 or 4 but the last variety with a 3 rating entered the RL in 1989. Only two varieties on the 2021/22 RL have a rating of 4, while 13 of the 33 varieties have ratings of 7 or 8. Even so, breeders will need to produce varieties with ratings between 6 and 8 consistently to achieve good Septoria control without having to rely routinely on fungicides.

Selection for Septoria resistance uses trial sites in mild, humid regions although a significant new challenge is the spread of yellow rust into areas where it was not formerly important. Not only is it inherently difficult to select resistance to one disease when another pathogen is present at high levels but also, it is surprisingly easy to confuse Septoria and yellow rust at certain stages of the two diseases' life cycles. There are many QTL for Septoria resistance in

European wheat (Brown et al., 2015; also see Riaz et al., 2020) but as none of them are especially important, it is unlikely that breeders use marker-assisted selection for specific genes. Knowledge of mechanisms of host defence against Septoria is limited (O'Driscoll et al., 2014), but that is not very important in the context of selecting for quantitative advances in varieties' resistance. Septoria resistance, as a highly important trait with complex genetic control, is very much the type of character which can be advanced by genomic selection. Even so, phenotypic selection for quantitative resistance may continue to be the mainstay of improvements in Septoria resistance but breeders will need to maintain and even expand the genetic diversity in their plant material to continue forming new, more effective combinations of minor genes to improve Septoria control.

Several major genes were present in UK wheat pedigrees up to 2000, notably *Stb15*, *Stb6* and, in spring wheat, *Stb9*, but they played little if any role in field resistance (Arraiano et al., 2009; Arraiano and Brown, 2017). Since then, some major genes have been used but probably only *Stb16q* has been introduced deliberately in the last decade (Saintenac et al., 2021). As with major genes for rust and mildew resistance, it was overcome within just a few years (Kildea et al., 2020). An unmapped gene was introduced in Cougar, possibly from a line derived from *T. dicoccoides*, but virulent isolates were detected in the UK in 2015 (Caiazzo et al., 2019). Higher levels of Septoria than expected from RL ratings were detected on varieties bred from Cougar in Ireland in 2020 (Kildea et al., 2021) and there was a similar report from the UK in 2021 (AHDB, 2021). Cougar-virulent isolates were recovered from such varieties in Ireland (Kildea et al., 2021). As ever with major genes, the Cougar resistance may have selected virulent genotypes of *Z. tritici* and is thus unlikely to be durable. No doubt such major genes will continue to be introduced from time to time and, like the mildew resistance of Robigus wheat or the brown rust resistance of NFC Tipple barley, they may make some contribution to disease control if they are combined with durable, polygenic, quantitative resistance.

Disease escape is important in the susceptibility of wheat varieties to Septoria. As a splash-borne pathogen, *Z. tritici* spreads upwards between leaf layers in the crop as conidia are carried by heavy raindrops. Shorter plants with closer-spaced leaves therefore tend to be more susceptible to Septoria while varieties with earlier leaf emergence also tend to be more susceptible as their upper leaves, which are critical for yield formation, can suffer more extensive symptoms (van Beuningen and Kohli, 1990; Arraiano et al., 2009).

### 8.2 Septoria nodorum blotch

Nodorum or glume blotch used to be an important disease of leaves and glumes of wheat. It is another disease which has been successfully controlled

by breeding in northwest Europe and is now only significant in Norway (Cowger et al., 2020). In the UK, it has become so insignificant that since 2021/22, varieties have not been rated for resistance to it (Fig. 1c in Brown, 2015). Resistant varieties were bred by phenotypic selection in the absence of detailed knowledge of genetics and information about the presence of toxin-sensitivity genes in UK varieties has only recently become available (Downie et al., 2018). In Norway, the toxin-sensitivity gene *Tsn1* was present in 45% of varieties and the matching SnToxA toxin in 69% of fungal isolates. There was some association between the presence of *Tsn1* and field susceptibility to nodorum, suggesting that resistance of Norwegian wheat could be raised by selecting against *Tsn1* (Ruud et al., 2018; Lin et al., 2020).

## *8.3 Tan spot*

Tan spot is a significant fungal disease in regions of northwest Europe with warm summers, including southern Scandinavia and parts of Germany and France but it is less severe there than in eastern Europe or central Asia. Resistance is, as usual, polygenic with identified QTL having moderate, additive effects. As in nodorum blotch, toxin receptor genes promote susceptibility to tan spot (Kollers et al., 2014). In the UK, tan spot is quite common but it rarely causes serious crop losses and can be controlled by agronomic methods. As it is transmitted from stubble and crop debris, tan spot may have been stimulated by the trend to cultivate by minimum tillage rather than ploughing (https://ahdb.org.uk/tanspot).

## *8.4 Eyespot*

Eyespot is a disease of moderate importance which attacks the stem base of cereal plants, causing lodging. Although it affects all cereals, it is most significant on wheat. As it is transmitted on crop debris, it is more time-consuming to run field trials for eyespot resistance than for wind-borne or splash-borne diseases. Two genes for eyespot resistance are present in UK winter wheat, of which the more important is *Pch1* on a chromosome segment introgressed from *Aegilops ventricosa* onto chromosome 7D of wheat (Pasquariello et al., 2017). Varieties with *Pch1* on the 2021/22 winter wheat RL have a mean rating 2.3 points higher than those without and breeders are able to test large populations for molecular markers closely linked to *Pch1*. A less potent gene, *Pch2* on chromosome 7A, was introduced into UK germplasm in Cappelle Desprez, the dominant variety in the early 1960s. *Pch1* and *Pch2* aside, resistance to eyespot is, as usual, controlled by polygenes dispersed throughout much of the genome (Lewien et al., 2018). The difficulty of trialling large populations and thus accumulating polygenes for resistance may explain why progress with selecting eyespot

resistance has been slower than for most other wheat diseases. It might seem surprising that *Pch1* has not been used more widely, as it is only present in three of the 35 varieties on the 2021/22 RL. This reflects in part the moderate importance of eyespot, so breeders have higher priorities but in addition, the *Ae. ventricosa* segment bearing *Pch1* also carries genes which reduce yield. Battalion, recommended in 2007/08, was probably the first commercially successful variety to have *Pch1* without the yield penalty (Summers and Brown, 2013) but this has not resulted in a surge of similar varieties.

### 8.5 Fusarium head blight

Fusarium head blight (FHB) is less important in northwest Europe than in areas of central and eastern Europe with hotter summers but it can be significant in wheat following a maize crop. More important than the effect of FHB on yield, however, is the requirement to reduce the level of the fungal toxin deoxynivalenol (DON) in harvested grain to as close to zero as possible. In the UK, FHB is of medium importance but that does not reflect its significance to breeding companies with operations throughout Europe. Breeders run field trials for resistance in areas where FHB epidemics are predictable, such as central Germany. This is combined with selection for anther extrusion, a trait strongly associated with reduced severity of FHB, while marker-assisted selection for QTL of moderate importance is economically worthwhile, given the high cost of running field trials for this disease. Breeders use the gene *Fhb1* because when pathogen pressure is low to moderate, it prevents the fungus spreading into the ear and thus limits DON accumulation (Buerstmayr et al., 2020). There may be scope for improving FHB resistance in future by selecting mutations in genes which promote susceptibility (Hales et al., 2020).

## 9 Resistance to non-biotrophic fungal diseases of barley

### 9.1 Net blotch and Rhynchosporium

Barley is affected by several non-biotrophic leaf spotting diseases, with symptoms that can be difficult to distinguish, even for an experienced pathologist. Net blotch resistance is one of the most important traits in winter barley, with high importance in malting barley and very high importance in feed barley, but is not considered important in spring barley. It is caused by two forms of one fungal species, *Pyrenophora teres* f. *teres* and f. *maculata*, which produce the netting and spotting forms of net blotch respectively. There has been more research on the more widespread netting form, although the spotting form is also common. Resistance to net blotch is polygenic and as usual, is characterised by several QTL with effects large enough to be identified as single genes, in addition to a presumably large number of dispersed genes

with small effects which have not been detected individually. Some resistance genes with larger effects have specific interactions with pathogen isolates, reflecting a possibly complex set of interactions between pathogen toxins and host receptors (reviewed by Clare et al., 2020).

Both winter and spring barley are attacked by *Rhynchosporium commune*, an ascomycete fungus which causes a disease known variously as leaf blotch, scald or most commonly, simply Rhynchosporium. It has very high importance in winter feed barley and high importance in winter malting barley and spring barley. Like net blotch and many other plant diseases, resistance involves polygenic quantitative resistance, including mapped QTLs as well as genotype-specific interactions, some of which are well characterised. Breeding for Rhynchosporium resistance has involved introgression of genes from wild barley as well as selection within cultivated germplasm (reviewed by Zhang et al., 2020).

The complex control of partial resistance is apparent in RL ratings for both these diseases (net blotch: Fig. 3c; Rhynchosporium: Figs 3d and 4b) as there has been a tendency for resistance ratings of most but not all varieties to decline over the years. This is consistent with evolution of pathogen virulence involving specific interactions with host resistance genes. Nevertheless, most current varieties have ratings which indicate moderate resistance to both diseases. Most winter barleys on the 2021/22 RL have ratings of 6 or 7 for net blotch and most winter and spring varieties have 5 or 6 for Rhynchosporium. The general pattern of resistance is consistent with a situation in which quantitative resistance is controlled largely by genes which provide durable resistance while some have effects which are moderately or weakly specific to certain fungal genotypes.

Despite quantitative resistance to net blotch and Rhynchosporium being less durable than mildew and brown rust resistance, some varieties are potentially reliable sources for use in barley breeding. Considering those that were on the RL for at least five years, Amarena, Boot, Camion and Colibri maintained ratings above 7.0 for net blotch resistance throughout their period of cultivation while several other varieties maintained ratings above 6 with little decrease in resistance. For Rhynchosporium in winter barley, Amarena, Pelican, Pict and Volume stand out as resistant over their commercial lifetime, as do Publican, Rebecca and Westminster in spring barley.

## *9.2 Ramularia leaf spot of barley: limits to breeding?*

Ramularia leaf spot has been recognised as a disease of barley for nearly 40 years but it is only 20 years since it was identified as a significant threat. It is a late season disease which primarily affects the top two leaf layers and can cause substantial losses to grain yield and quality. When it first became

commercially important, it was quickly realised that all the most susceptible varieties had *mlo* mildew resistance (Havis et al., 2015). In genetic analysis of a biparental cross, the mildew-resistance allele *mlo11* increased susceptibility to Ramularia at sites in Bavaria, Scotland and Norway, although the effect was somewhat variable (McGrann et al., 2014). There were advances in selecting for Ramularia resistance until the early 2010s but since then, progress has stalled.

A brief summary of the current situation is that, first, modern spring barley varieties are not as susceptible as many *mlo* varieties in the early 2000s so it seems that, as in other cereal diseases, breeders have successfully eliminated very susceptible genotypes. Ramularia resistance was rated on the barley RL in 2017/18 and 2018/19 but in trials across the UK, there was great variation in the relative susceptibility of varieties at different locations, even at sites which were close to one another. The average ratings in the RL therefore did not give a reliable prediction of varieties' responses to Ramularia on farms. The size of the GxE effect, which is much larger than variation between varieties' average susceptibility, explains why breeders have not been able to make further significant advances since culling the highly susceptible *mlo* lines.

The fungal pathogen, *Ramularia collo-cygni*, has been associated with barley since at least the mid-nineteenth century (Fountaine and Fraaije, 2009). The key point may not be to develop varieties which are resistant to Ramularia in current farming conditions so much as to understand why, after decades or centuries as an apparently harmless endophyte, *R. collo-cygni* became an aggressive parasite in the mid-1990s. The important questions may be agronomic, not genetic: what features of agriculture changed around that time, did they provoke *R. collo-cygni* to become a pathogen, and can they be reversed?

## 10 Resistance to viral diseases

Two types of viral disease are significant in cereals in northwest Europe, soil-borne mosaic viruses and the aphid-transmitted Barley yellow dwarf virus (BYDV).

### 10.1 Soil-borne mosaic viruses

Greatest progress has been made in breeding for resistance to Barley yellow mosaic virus (BYMV) and Barley mild mosaic virus, Bymoviruses which are transmitted by the slime mould *Polymyxa graminis*. Phenotypic selection for resistance requires a trial site infested with the virus, so marker-assisted selection for the resistance gene is preferred. All winter barley varieties released recently in the UK have resistance to both viruses, probably conferred by the recessive gene *rym4* (Fig. 3e). Although this resistance has been effective to

date, resistance-breaking strains have been found in fields of *rym4* varieties (Rolland et al., 2017). Other *rym* genes, particularly *rym5* at the same locus as *rym4*, are being used in barley breeding. The slow dispersal of soil-borne mosaic viruses means it should be feasible to control BYMV with major genes because when a resistance-breaking strain appears, breeders have time to select other resistance genes (Ordon et al., 2009).

The most significant soil-borne virus of wheat is Soil-borne cereal mosaic virus (SBCMV). Resistance is provided by *Sbm1* on chromosome 5D and *Sbm2* on 2B, which are both present in the resistant variety Cadenza (Bayles et al., 2007). Cultivars had similar resistance at sites in France, Italy and the UK, indicating that SBCMV resistance should be useful in breeding across Europe (Budge et al., 2008).

### 10.2 Barley yellow dwarf virus

The aphid-borne pathogen BYDV has recently and quite suddenly become a cause for serious concern on all cereals, following the EU-wide ban on using neonicotinoid insecticides for crop protection in 2018 (European Commission, n.d.). This has generated strong demand for BYDV-resistant varieties. The first resistant wheat variety in the UK, RGT Wolverine, was recommended in 2021. Field selection for a resistant phenotype will only be reliable if viruliferous aphids become more common than they are at present, so marker-assisted selection for known genes is essential. RGT Wolverine has the *Bdv2* resistance gene, introgressed into wheat chromosome 7D from a wild grass, *Thinopyrum intermedium* (Zhang et al., 2009).

## 11 Resistance to insects

Aside from their role as vectors of pathogenic viruses, some insects are pests of cereals in their own right. In recent years, the most significant has been *Sitodiplosis mosellana*, the orange wheat blossom midge (OWBM), a gall midge. The yellow or lemon wheat blossom midge, *Contarinia tritici*, is also found in the UK but is rarely damaging (https://ahdb.org.uk/knowledge-library/how-to-identify-wheat-blossom-midges). OBM has a long-lived pupal phase so its numbers can be reduced by crop rotation and cultivation, but the most effective way of controlling it is by growing resistant varieties. *Sm1* on chromosome 2B of wheat provides strong resistance to OBM (Kassa et al., 2016) and has been used increasingly in European breeding. It is currently present in 23 of 33 winter wheat varieties on the 2021/22 RL, including all those in the soft endosperm Groups 3 and Soft 4, and in three of the eight spring varieties, all of which have hard endosperm (Fig. 7). Resistance is associated with greater induction of phenolic acids such as ferulic acid and *p*-coumaric acid during

early grain development (Ding et al., 2000). All breeders select *Sm1* by marker-assisted selection.

As well as being vectors of BYDV, aphids used to be important pests of wheat in their own right before the introduction of modern insecticides. Resistance of the most important aphid, the grain aphid *Sitobion avenae*, to pyrethroid insecticides is widespread in England (Foster et al., 2012) and Ireland (Walsh et al., 2020). This involves a significant fitness cost but nonetheless will threaten aphid control if pyrethroids are used heavily instead of neonicotinoids. Research in the 1970s detected significant variation in resistance of wheat and barley to *S. avenae*, with the popular wheat variety Maris Huntsman being particularly susceptible (Lowe, 1980). In principle, therefore, it will be possible to breed cereal varieties with greater resistance to aphids but a significant challenge is to scale up the tests so that enough plants can be scored even to select resistant parents, let alone improved progeny lines.

## 12 Mitigating trade-offs of disease resistance

Disease resistance which involves induction of plant defences may be energetically costly. Fitness costs of resistance and their relevance to plant breeding were reviewed by Brown and Rant (2013). While one might intuitively suppose that such costs could limit the ability to increase quantitative resistance, the examples and data presented here show that if there are such costs in European cereal varieties, they have not been large enough to prevent
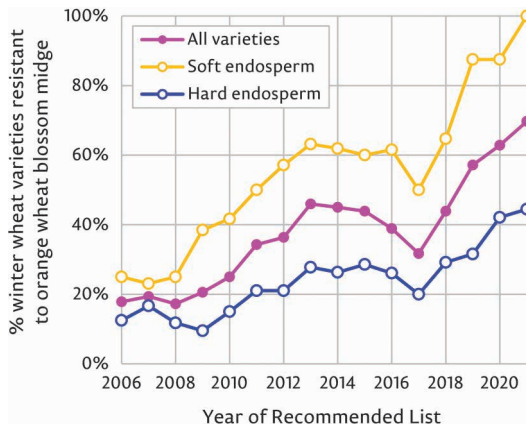


**Figure 7** The proportions of winter wheat varieties with resistance to orange wheat blossom midge from 2006, when this trait was first included in the Recommended List. Resistant varieties are those that breeders claim to have *Sm1* based on DNA sequence data. Soft endosperm varieties are in Group 3 and Soft Group 4; hard endosperm varieties are in Group 1, Group 2 and Hard Group 4.

breeders from increasing yield and maintaining quality while simultaneously developing durable resistance to most diseases.

## 12.1 The best alleles in the best genomes

*mlo* mildew resistance in spring barley gives an insight into how fitness costs may affect cereal breeding (reviewed by Brown and Rant, 2013; also see McGrann et al., 2014; Gruner et al., 2020; Jacott et al., 2020). *mlo* mutations incur large yield penalties, increase susceptibility to some non-biotrophic diseases and decrease mycorrhization. The penalties of most artificial alleles are greater, however, than those of the natural allele *mlo11* and one of the artificial alleles, *mlo9*, which have been widely used in breeding. The first point, therefore, is that the process of accelerated natural selection that operates in plant breeding programmes enables breeders to select the alleles which have the largest benefits compared to any costs. In a segregating population of a cross of an *mlo5* line with one carrying wild-type *Mlo* (*Mlo*+), it was possible to select lines which had *mlo5* as well as grain yield close to that of the *Mlo*+ parent (Kjær et al., 1990). The second relevant point, therefore, is that breeders can select lines in which reassortment of background genes modifies the effect of *mlo* on traits other than mildew resistance. The rest of the genome is thus adapted to the presence of the *mlo* allele, reducing the penalties of the strong mildew resistance. Yields of the best *mlo11* lines are now not much lower than those of *Mlo*+ varieties but I understand from several barley breeders that crosses between the two genotype classes are rarely productive.

One can readily imagine that the same process applies to breeding for disease resistance in general. When breeders select an optimal phenotype, they are selecting alleles of disease resistance genes which have the greatest benefit in relation to any costs, and they are also reassorting the genome to minimise any remaining costs. In this way, if there are costs of durable resistance, they do not matter. At least, they have not prevented successful breeding for resistance to most diseases of cereals.

## 12.2 Disease escape

Disease escape results from the effects of crop morphology or development on disease progress. The spread of splash-borne diseases such as Septoria tritici blotch and Septoria nodorum blotch can be promoted by shorter plant height, earlier flowering, larger leaves and leaf layers overlapping so that spores are more easily transmitted from one leaf to the other (Scott et al., 1982; van Beuningen and Kohli, 1990; Lovell et al., 2004; Arraiano et al., 2009; Judge, 2015). Disease escape traits can be seen as costly because the ideal plant

ideotype from the point of view of yield formation may be one which promotes disease: earlier leaf emergence, longer-lived leaves and larger leaves allow photosynthesis over a longer time or larger area, while shorter plants divert more photosynthate to the ear instead of vegetative tissue. Genes on chromosome 6A are associated with larger, longer-lived leaves and thus greater yield but this also results in greater severity of Septoria (Judge, 2015; Arraiano and Brown, 2017). Breeders need to balance maximising yield against minimising the cost of disease control. Selecting stronger disease resistance will reduce the relevance of disease escape and thus give breeders greater flexibility to modify developmental and morphological traits in such a way as to increase yield.

## 13 Future threats

### 13.1 Stem rust: a known unknown

In the epistemiological system of the late Donald H. Rumsfeld, the examples above are the 'known knowns' of cereal diseases: those we know can cause trouble. The outstanding disease among 'known unknowns' – those that are absent or not currently severe but may become more serious – is black or stem rust of wheat (*Puccinia graminis*). This has been largely absent from northwest Europe since the 1950s but has been found occasionally in this region in recent years (Lewis et al., 2018; Hovmøller et al., 2021). The most significant factor suppressing stem rust over the last 60 years may have been earlier harvesting of wheat, made possible by selection for earlier maturity (another example of disease escape driven by crop development). In future, the warmer summer weather that will result from climate change may make the northwest European environment more conducive for stem rust (Lewis et al., 2018).

UK wheat varieties are susceptible to stem rust (Lewis et al., 2018) and given the close relationship between UK varieties and those elsewhere in Europe, the same is probably true of other countries in this region. If stem rust becomes more common in northwest Europe, stronger, durable resistance will be needed. Breeders can take advantage of the globalisation of their industry to run trials for resistance to a disease in locations where it is common, aiming to select resistant lines before the pathogen becomes troublesome in northwest Europe. In pre-emptive breeding trials, European varieties can be tested in places where there are reliable epidemics of stem rust caused by genetically diverse populations of *P. graminis* f.sp. *tritici*. Lines which are susceptible to as many pathogen genotypes as possible with a high infection type as seedlings, but have low stem rust severity in field conditions, are likely to have race-non-specific, quantitative, probably durable resistance (for similar work on mildew of wheat in central China, see Yu et al., 2001). If such trials are run regularly over the next 20-30 years and if breeders are prepared to discard varieties which are

excessively susceptible to stem rust, there is a good chance of building up an acceptable level of durable resistance to the disease before it re-emerges as a serious problem in northern Europe.

Oat stem rust (*P. graminis* f.sp. *avenae*) has re-emerged in Sweden following the repeal of a law requiring eradication of barberry in 1994 (Berlin et al., 2013). This has allowed the pathogen to complete its sexual cycle in Sweden and has resulted in outbreaks of oat stem rust being more frequent and occasionally severe. Despite the value of barberry to wildlife, those benefits should be balanced against the risks to production of cereals, including wheat and barley as well as oats. Perhaps eradicating barberry from hedgerows around arable fields would be an acceptable compromise.

### 13.2 Unknown unknowns

By contrast, 'unknown unknowns' are organisms which are not known to be major threats to crop production, perhaps because their potential for causing damage in northwest Europe is not appreciated or because they are not favoured by the current environment or agronomy. New, previously unknown diseases must be combatted by a broad range of methods because it takes several years to breed for resistance to them. It is not possible to breed for resistance to a pathogen the existence of which we do not yet know. When Ramularia leaf spot of barley, the most prominent new disease of cereals in recent decades, first became serious around 2000, it was quickly found that broad-spectrum fungicides which were active against many other ascomycete fungi also controlled *R. collo-cygni*. This gave breeders time to eliminate the most susceptible varieties. Breeders need to work closely with agronomists to control new diseases (as they did in the case of Ramularia), but agronomists need to have access to a reasonably wide range of pesticides to buy time for breeders (Brown, 2008). The fundamentals of breeding for resistance to a new pathogen are the same as those for established diseases: genetically diverse but well-adapted germplasm, an effective trialling system including locations where the disease is prevalent, and an efficient process for improving resistance to the new pathogen in germplasm with high yield, good quality, suitable agronomic properties and low susceptibility to other pests and diseases.

## 14 Acknowledgements

## 15 Where to look for further information

AHDB has a large Knowledge Library with information about almost all pests and diseases relevant to arable farming in the UK. Much of it is also relevant to other countries in northwest Europe. Go to: https://ahdb.org.uk/knowledge -library and filter first by Cereals & Oilseeds then by Crops & Grassland and a topic such as Diseases, Pests or Varieties. Or search by the name of a disease as a keyword.

Recommended Lists are available at: https://ahdb.org.uk/rl for the current year and https://ahdb.org.uk/rlarchive for previous years back to 2004/05.

The AHDB's Variety Selection Tool is at: https://ahdb.org.uk/vst.

Information about the plant breeding industry in the UK, which is closely integrated with companies elsewhere in Europe, is produced by the British Society of Plant Breeders at: https://bspb.co.uk/.

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