J Plant Dis Prot (2025) 132:58
https://doi.org/10.1007/s41348-024-01049-y

SHORT COMMUNICATION

# Prevalence of key resistance alleles associated with DMI and SDHI fungicide resistance in European *Zymoseptoria tritici* populations in 2022

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Received: 22 September 2024 / Accepted: 14 December 2024 / Published online: 8 January 2025

## Abstract

In Northern Europe, the application of fungicides to winter wheat crops is primarily for the control of septoria tritici blotch (STB) caused by the fungal pathogen *Zymoseptoria tritici*. Unfortunately, intensive use of the demethylation inhibitors (DMI) and succinate dehydrogenase (SDHI) fungicides has led to the development of resistance in the European *Z. tritici* population. Levels of disease control achieved by both modes of action are partly dependent on the presence and frequencies of specific alleles, including CYP51-S524T, SDHC-T79N, C-N86S and C-H152R, in the population. To determine how frequent these are across the major wheat producing regions of Europe, a survey of *Z. tritici* was conducted in 2022, using specific qPCR assays to detect the frequencies of each allele. A west–east gradient of resistant allele frequencies was observed, with higher levels observed in the west. Comparing frequencies detected to a previous survey conducted in 2019 confirms the continued evolution of fungicide resistance in the European *Z. tritici* population. To ensure the continued effectiveness of these fungicides, it is essential ensure they are applied as part of an integrated disease control strategy that aims to reduce the overall need for their application.

**Keywords** *Mycosphaerella graminicola* · Sensitivity · Disease control · Septoria tritici blotch · Triazole · Wheat

## Introduction

Septoria tritici blotch (STB), caused by *Zymoseptoria tritici,* continues to be among the most economically destructive diseases of winter wheat crops throughout Northern Europe. Control strategies rely heavily on the combination of host genetics and fungicides, with the majority of fungicides applied to winter wheat across the region primarily for the control of STB (Fones & Gurr 2015, O'Driscoll et al., 2014). These fungicides predominantly belong to the demethylation inhibitor (DMI; FRAC Group 3; e.g., mefentrifluconazole & prothioconazole) and succinate dehydrogenase inhibitor (SDHI; FRAC Group 7; e.g., fluxapyroxad, bixafen, benzovindiflupyr) fungicide modes of action. Both contain somewhat chemically diverse active ingredients, with varying levels of activity toward *Z. tritici*, dependent on the affinity between each chemical and the fungal target.

The fungicidal activity of DMIs is realized through disruption of ergosterol production by inhibition of the enzyme 14α-demethylase (CYP51). Together, with the overexpression of CYP51 and enhanced fungicide efflux, increasingly

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complex combinations of amino acid alterations in CYP51 have been identified as key contributors to reducing the sensitivity of *Z. tritici* to the DMI fungicides (Cools and Fraaije 2013; Omrane et al. 2017; Huf et al. 2018; Kildea et al. 2019, 2023, 2024). The diverse nature of the DMI group and their heterogeneous use in wheat crops across Europe have led to the emergence of populations containing highly diverse CYP51 haplotypes, often with slight differences in sensitivity to the different DMIs, depending on population composition (Hellin et al. 2021; Jørgensen et al. 2021). Indeed, CYP51 combinations of alternations may determine the spectrum of cross-resistance between DMI fungicides as well as the level of sensitivity to each compound. However, intensive European monitoring, heterologous expression studies, in silico molecular docking studies and applied predictive modeling suggest that alterations at position 136 (V136A/C), I381V and most notably S524T are key predictors of DMI overall field efficacy (Cools et al. 2011; Cools & Fraaije 2013, Kildea et al. 2023).

The SDHIs specifically target fungal respiration by inhibition of succinate dehydrogenase (SDH), a key protein involved in the mitochondrial election transportation within complex II and hence respiration. As for the DMIs, the SDHIs are becoming an increasingly chemically diverse mode of action and a variety of alterations with varying degrees of impact on sensitivity has been identified in *Z. tritici* across the SHD complex (subunits B, C, and D) (FRAC 2024. This diversity includes the alterations C-T79N, C-N86S, and C-H152R (Rehfus et al. 2018). Differences in sensitivity have been observed between these alterations, with C-H152R conferring the greatest reductions in sensitivity (Dooley et al. 2016; Hellin et al. 2021; Rehfus et al. 2018).

The impact these different alterations have on field efficacy of the DMI and SDHI fungicides is dependent on their frequencies in a given population (Blake et al. 2018). The differences in efficacy apparent across Europe, as identified as part of the EUROWHEAT trials network support this, with lowest levels of efficacy observed in the United Kingdom and Ireland where the prevalence of the different alterations was greatest in the respective trials (Jørgensen et al. 2022). This gradient in frequency of the key alterations that impact efficacy of the SDHIs: C-T79N, C-N86S, and C-H152R, the DMIs: CYP51-S524T and QoIs: G143A was previously identified in a study conducted prior to the application of fungicides in spring 2019 (Hellin et al. 2021; Kildea et al. 2022). Major changes in the availability of fungicides in the European cereal fungicide market has occurred since then. This has included the revocation of the multisite chlorothalonil, which was a major component of STB control across most EU countries and less prone to resistance selection, the introduction of the novel Quinone inside Inhibitor (QiI) fenpicoxamid (Owen et al. 2017) and the DMI mefentrifluconazole (Strobel et al. 2020). These changes in availability have dramatically changed the overall fungicide landscape in European winter wheat crops and as such it is imperative to determine the current status of the key resistance alleles. Having such information is essential to ensure fungicide programs are devised that both maximize their efficacy but at the same time preserve it while delaying resistance.

Here, we report the findings of an intensive monitoring program undertaken in the summer of 2022. Based on previously published information relating to the different alterations associated with DMI and SDHI resistance in *Z. tritici*, and using the allele and species-specific protocols and markers developed by Hellin et al. (2020) and Hellin et al (2021) we screened Northern-European *Z. tritici* populations for frequencies of the alteration CYP51-S524T associated with DMI resistance, and the alterations C-T79N, C-N86S and C-H152R associated with resistance to the SDHIs. The specific countries selected represent the range of disease pressures and fungicide selection that exist in the region, and frequencies of the key alterations detected suggest a continued erosion of sensitivity to both the DMIs and SDHIs.

## Materials and methods

### Field sampling

At the end of 2022 cropping season, 82 wheat fields were sampled for STB symptoms throughout 10 European countries (Tables S1), typically around growth stage BBCH 73–85. In each field, a single symptomatic leaf with visible pycnidia was sampled every 10–20 m, either along a W-shaped path across the fields or along the tram lines established in the field, with between 50 and 80 leaves sampled per field. Individual leaves were grouped together to represent the local population. Samples from France originated from trial fields of the “Réseau Performance” (Garnault et al. 2019) and were picked in treatments plots corresponding to typical French fungicide programs. The latter also applies to the samples from Germany, with treatments that reflect typical fungicide strategies for southern Germany. All other samples were retrieved from commercial fields which had received fungicides. Leaves were air-dried for a minimum of 48 h and stored in paper envelopes at room temperature before further processing.

### Resistance allele frequency determination in leaf samples

A single 2-mm leaf plug was taken from one STB lesion on each leaf using a biopsy puncher. All leaf plugs originating from the same field were pooled (40 to 50 per field), and DNA was extracted centrally at Aarhus University using a KingFisher DNA extraction system with a MagMax DNA extraction kit in accordance to the manufactures instructions (ThermoFisher Scientific,) and as described previously by Hellin et al. (2021). The frequency of four alleles, known to confer reduced sensitivity or resistance to the DMI (CYP51-S524T) and SDHIs (C-T79N, C- N86S and C-H152R) fungicides in *Z. tritici* were determined in each sample using two allele and species-specific qPCR assays. The frequencies of CYP51-S524T and C-H152R were determined using the qPCR assay developed by Hellin et al. (2020), with frequencies of C-T79N and C-N86S determined using a similar assay developed by Hellin et al. (2021), with minor modifications as follows. The four probes targeting the alleles C-T/N79 C-N/S86 and respective primer pair as per Hellin et al. (2021) (Supplementary Table), were combined in a single multiplex reaction, with final concentrations of 250nM for the probes and 400 nM for the primers in mixture. All reactions were performed in duplicates using Takyon No Rox Probe MasterMix dTTP Blue (Eurogentec, Belgium), in a CFX96 Real-Time PCR detection system (BioRad, USA), with the intensity of fluorescence captured at the end of each cycle, as per Hellin et al. (2021). All PCR runs included controls of the respective alleles being assessed. Frequencies of each allele in the test samples was determined by computing the ratio between the quantity of mutant for this allele, given by the respective probe signal, and the total quantity of *Z. tritici* DNA, deduced from the signals from both probes targeting the same locus.

### Statistical analysis

Differences between the countries in terms of the frequencies of the four resistance alleles were determined using a Kruskal–Wallis test, with comparisons between them subsequently determined using Dunn's test with Bonferroni correction. To determine if the frequencies of the four resistance alleles have changed at an individual country level since 2019, Welch t-tests ($\alpha = 0.05$) were conducted using the frequencies established in 2019 (Hellin et al. 2021) and those established in the present study. For this analysis, only countries with greater than five fields sampled in each year were included. All statistical and graphical analysis was conducted using R programming language (R Core Team 2018) with the packages "tidyverse", "FSA", "agricolae", "ggplot2" and "egg". Mapping of the different allele frequencies was produced using QGIS3.0.

## Results

### Frequencies of selected resistance alleles across Northern Europe in 2022

For three of the four alleles (CYP51-S524T, C-T79N, and C-N86S) targeted, significant differences in their frequencies present in the different countries screened were detected ($P < 0.05$). The Irish population had the highest mean frequencies (89%, 30% and 64%, respectively) of the alleles among the countries tested (Table 1, Fig. 1), with the lowest levels detected in Eastern Europe (Estonia (17%, 4% and 11%, respectively), Latvia (30%, 5% and 24%, respectively) and Slovenia (0.3%, 0.7% and 0%, respectively). Other countries exhibited intermediate frequencies (CYP51-S524T: 26–52%; C-T79N: 4–9%; C-N86S: 25–55%). For each of these three resistance alleles, a west to east longitudinal gradient was evident in Europe (Fig. 1; Table 1).

For C-H152R, no significant difference ($P > 0.05$) was detected between the countries in terms of the frequency of the allele in the populations, with the maximum mean frequency detected in Germany (4%). While the mean country frequencies were extremely low, ranging from < 0.01–4%, in some countries (France, Germany and Ireland), individual field populations harboring > 10% SDHC-H152R were detected (Table 1).

### Changes in frequencies of selected alleles between 2019 and 2022

As the detection methods used were as per Hellin et al. (2021), it was possible to monitor how the frequencies of the different resistance alleles in Belgium, Denmark, France, Ireland and Sweden has changed between 2019 (early spring) to 2022 (end of summer) (Fig. 2). For each of the five countries there was a significant increase in the frequencies of CYP51-S524T and C-N86S alterations between both sampling points ($P < 0.05$). For C-T79N significant increases in the frequencies detected were observed in Belgium, France and Sweden ($P < 0.05$), although the mean frequencies detected in 2022 remained below 10% for each country. A significant increase in the C-H152R alteration was only observed in Belgium, although its overall detection remained low, at 4%.

## Discussion

As both the DMI and SDHI fungicides remain critical to the control of STB across Northern Europe, it is essential to continually monitor for changes in the frequencies of

**Table 1** Frequencies of CYP51-S524T and SDH C-T79N, C-N86S and C-H152R in *Zymoseptoria tritici* populations detected using qPCR throughout European winter wheat fields in summer 2022

| Country (# of fields) | CYP51-S524T | | | | SDHC-T79N | | | | SDHC-N86S | | | | SDHC-H152R | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Detection | Mean | Min | Max | Detection | Mean | Min | Max | Detection | Mean | Min | Max | Detection | Mean | Min | Max |
| Belgium (7) | 100.0 | 42.9 | 19.8 | 54.5 | 100.0 | 9.1 | 3.5 | 12.1 | 100.0 | 54.7 | 39.9 | 73.4 | 100.0 | 3.5 | 0.0 | 9.3 |
| Denmark (8) | 87.5 | 26.7 | 0.0 | 40.8 | 100.0 | 3.6 | 0.2 | 12.4 | 87.5 | 35.5 | 0.0 | 56.8 | 25.0 | 0.0 | 0.0 | 0.1 |
| Estonia (5) | 100.0 | 16.5 | 1.2 | 31.6 | 60.0 | 4.1 | 0.0 | 11.4 | 40.0 | 11.0 | 0.0 | 54.6 | 20.0 | < 0.01 | 0.0 | 0.0 |
| France (18) | 100.0 | 25.9 | 1.4 | 66.2 | 100.0 | 5.2 | 0.1 | 22.2 | 88.9 | 41.4 | 0.0 | 93.1 | 50.0 | 2.1 | 0.0 | 16.4 |
| Germany (3) | 100.0 | 51.0 | 34.4 | 60.1 | 100.0 | 8.4 | 5.9 | 10.0 | 100.0 | 43.3 | 21.7 | 73.3 | 66.7 | 3.8 | 0.0 | 11.1 |
| Ireland (20) | 100.0 | 89.5 | 46.3 | 98.4 | 100.0 | 29.5 | 2.2 | 77.5 | 100.0 | 63.7 | 20.8 | 97.0 | 70.0 | 3.5 | 0.0 | 34.7 |
| Latvia (5) | 100.0 | 30.0 | 15.3 | 50.6 | 100.0 | 4.9 | 0.7 | 11.1 | 100.0 | 23.7 | 0.8 | 61.3 | 60.0 | 0.1 | 0.0 | 0.3 |
| Poland (2) | 100.0 | 52.3 | 32.0 | 72.6 | 100.0 | 4.4 | 1.8 | 7.1 | 100.0 | 24.8 | 22.7 | 27.0 | 100.0 | 0.3 | 0.1 | 0.5 |
| Slovenia (3) | 66.7 | 0.3 | 0.0 | 0.8 | 66.7 | 0.7 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 66.7 | 0.1 | 0.0 | 0.3 |
| Sweden (11) | 100.0 | 20.7 | 5.8 | 43.7 | 100.0 | 7.2 | 3.0 | 12.8 | 100.0 | 41.4 | 17.3 | 64.9 | 90.9 | 1.7 | 0.0 | 8.0 |

alterations associated with resistance to either fungicide groups in *Z. tritici* populations across the region. Using the markers developed by Hellin et al. (2021), we observed a west–east divide at the end of the 2022 growing season in the frequency of three of the four key resistance alleles monitored; CYP51-S524T, C-T79N, C-N86S. Understanding the driving forces for these changes and potential implications these changes may have on efficacy will be important to ensure control of STB. The alteration SDHC-H152R was first detected in field populations at the end of the 2015 field season in Ireland (Dooley et al. 2016), and even though it confers a high degree of resistance to all commercially available SDHI fungicides and is often detectable in field populations throughout Europe, as presented here and previously by Hellin et al. (2021), it has not been rapidly selected. It has been proposed that this may in part be due to a potential fitness penalty associated with resistance (Scalliet et al. 2012). The detection of the allele at frequencies > 10%, including a single field in Ireland at 34.75%, may suggest that strains with this allele may overcome this potential fitness penalty under strong disease and selection pressure. Unlike the previous study of Hellin et al. (2021), the samples analyzed here were collected at the end of the season and it may not have provided the opportunity for the potential fitness penalty associated with C-H152R to manifest themselves at a population level. Even with the presence of C-H152R at elevated levels in a small number of sites, it is encouraging that, with the exception of Belgium, there has been no significant increase in the allele since the previous study of Hellin et al. (2021) conducted three years previous, in 2019. This situation may result from the establishment of a beneficial trade-off between winter conditions that reshuffle population composition, and the positive selection exerted during the growing season by current practices in favor of a diversity of alleles with a low to moderate impact rather than C-H152R. It will be important to further understand this potential trade-off so that it is not destabilized resulting in its selection and expected decreases in SDHI efficacy associated.

Even in the absence of high levels of SDHC-H152R, Jørgensen et al. (2022) have reported significant decreases in the efficacy of the main SDHI fungicides against STB in both Ireland and the UK, where *Z. tritici* populations have high frequencies of the SDHC alleles C-T79N and C-N86S. Even though both alleles only confer what is deemed a moderate level of resistance (Dooley et al. 2016; Rehfus et al. 2018), when present at high frequencies in individual crops they can present difficulties in terms of maintaining efficacy from these fungicides. The exact frequency at which efficacy starts to be impacted is unknown, however with the exception of Poland and Slovenia, there were individual fields in the remaining countries where the frequency of SDHC-N86S was > 50% (Table 1). Care must be taken when

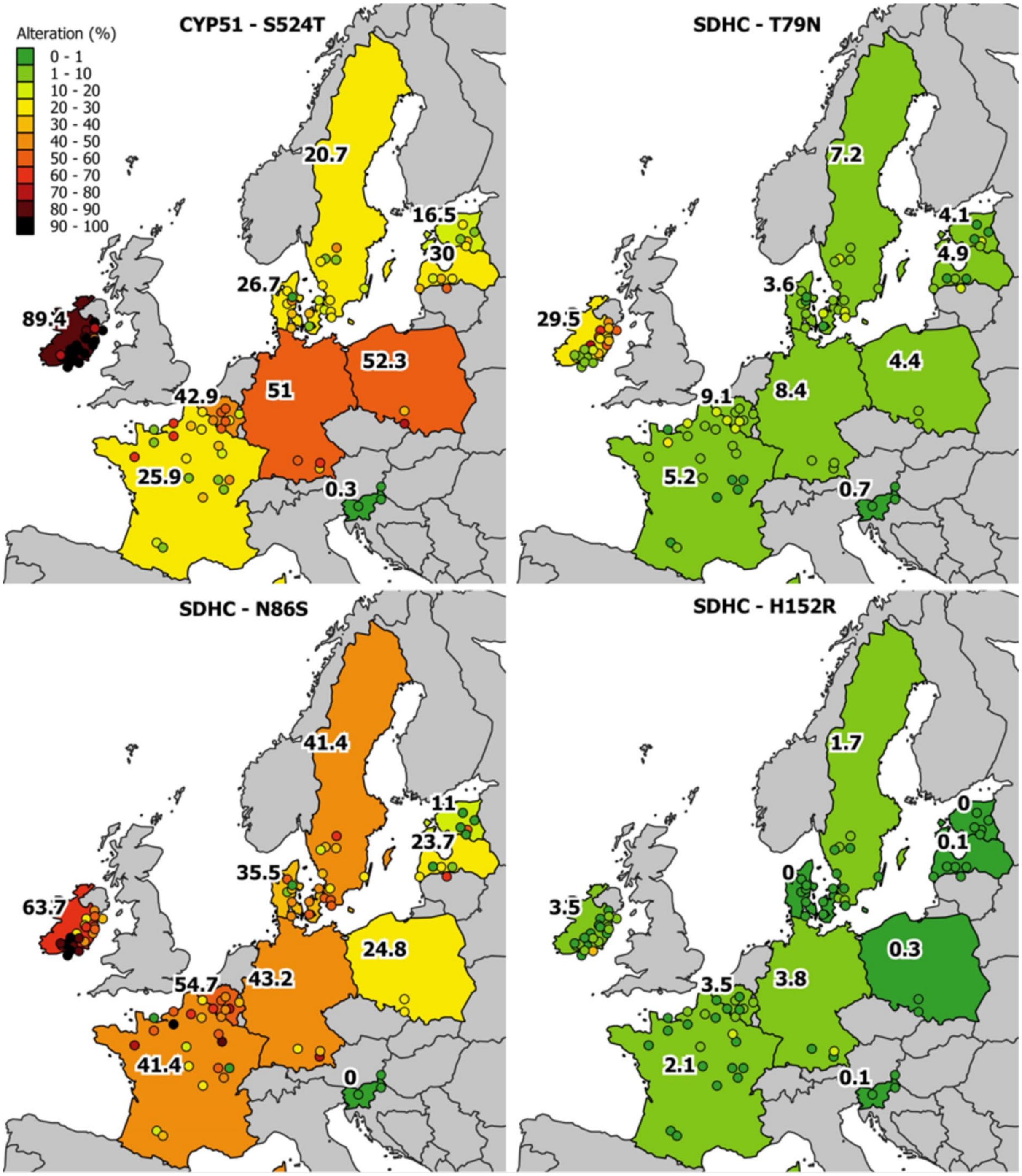

**Fig. 1** Frequencies of the DMI resistance allele CYP51-S524T and SDHI resistance alleles SDHC-T79N, C-N86S and C-H152R alleles in European *Zymoseptoria tritici* populations in 2022. Frequencies determined using qPCR assays developed and reported by Hellin et al. (2021)

assuming the continued efficacy of the SDHIs. Strategies such as mixing with alternative modes of action need to be implemented to ensure disease control is maintained.

It is interesting to note that limited selection has occurred across Europe for SDHC-T79N as compared to SDHC-N86S, although C-T79N was first selected in many countries and exhibits little fitness penalties. Other than in Ireland, no individual field-population harbored more than 22% of the SDHC-T79N allele. In Ireland, as has been previously reported by Hellin et al. (2021), the population appears to be structured, with fields in the east of the country dominated by strains of *Z. tritici* carrying SDHC-T79N, while those further west and south are dominated with strains with SDHC-N86S. A similar spatial difference has also recently been

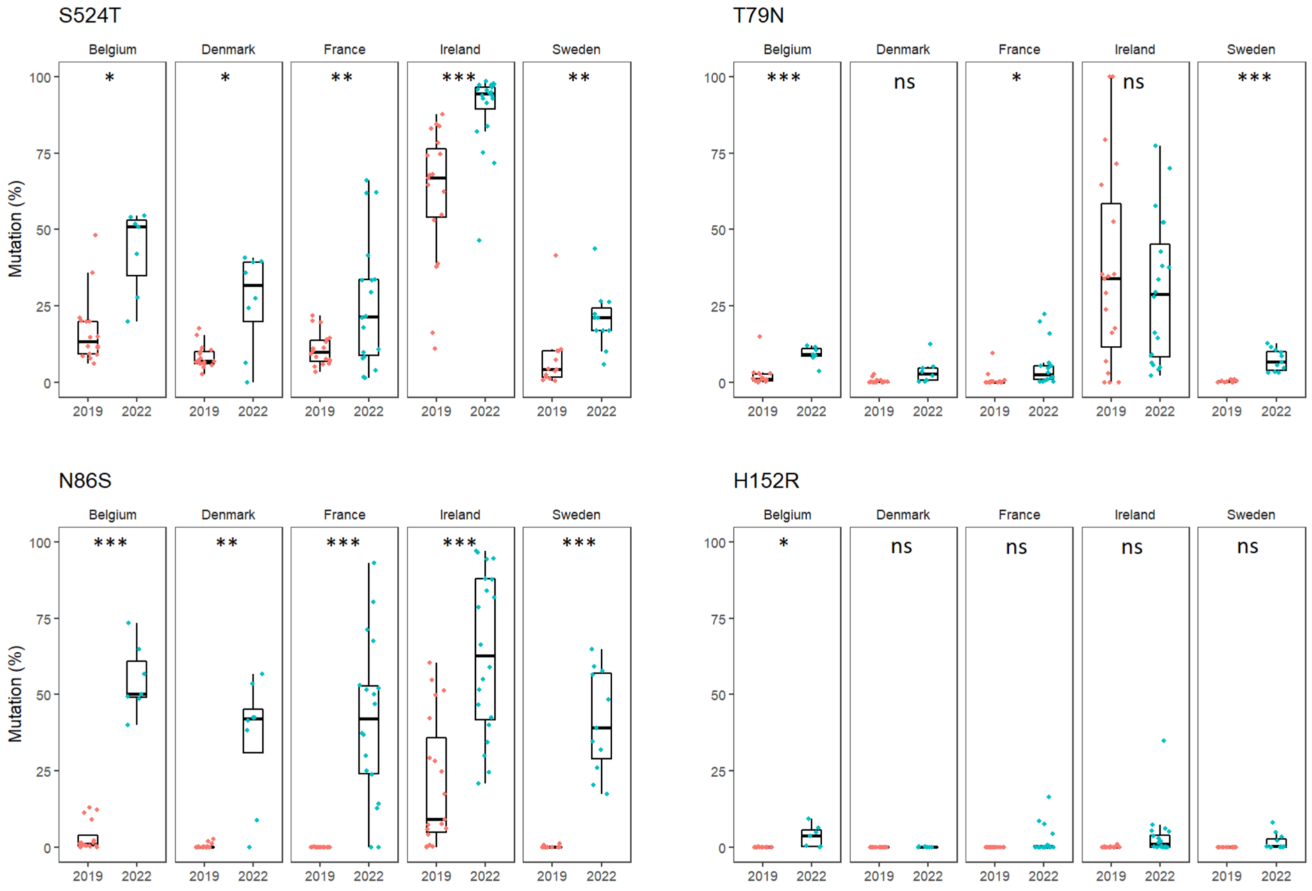

**Fig. 2** Changes in frequencies of the DMI resistance allele CYP51-S524T and SDHI resistance alleles SDHC-T79N, C-N86S and C-H152R alleles in Belgium, Denmark, France, Ireland and Sweden between 2019 and 2022. Frequencies for 2019 as per reported by Hellin et al. (2021), with frequencies for 2022 generated in the present study. Significant differences determined using Welch t-tests and presented as $* = P < 0.05$, $** \ P < 0.01$ and $*** \ P < 0.001$

reported by Kildea et al. (2024), except this was based on the sensitivity to the DMI fungicides mefentrifluconazole, prothioconazole-desthio and tebuconazole, and diversity of CYP51 haplotypes. No such population structure is evident in the other countries analyzed in the present study. Previous work by Garnault et al. (2019) has demonstrated such differences based on phenotype assessment have existed in France, with the authors hypothesizing that these were reflective of local fungicide usages and environmental factors. Given the STB pressures that can exist in Ireland, the use of fungicides in Irish winter wheat crops is homogenous, with similar products, application frequencies and rates of SDHI fungicides used irrespective of region. It can be expected that over time as local populations intermix these regional differences will dissipate, although as neither allele confer a major fitness advantage over the other in the presence of the SDHI fungicides it may not be a rapid increase/decreased in either.

Unlike C-T79N, with the exception of Slovenia, moderate-high frequencies of C-N86S were detected in each of the countries tested. While there were numerous fields with high frequencies (> 50%), there were equally fields in Denmark, France, Estonia and Slovenia where C-N86S was not detected. Among the five countries where it was possible to compare populations from 2019 and 2022, the frequency of C-N86S increased significantly in each of them. In most cases this increase likely reflects the continued use of SDHI fungicides for the control of STB and/or other cereal diseases between the two collection dates. However, the increase of C-N86S in Denmark from an overall mean of 0.37% in 2019, to 35.5% in 2022 is somewhat surprising given the limited availability and overall application of the SDHI fungicides to Danish winter wheat crops (https://middeldatabasen.dk/positiveList.asp, accessed 05.09.2024).

A wide range in the frequency of CYP51-S524T was detected across the region, with the west–east gradient very apparent (from 89.45 in Ireland to 0.29% in Slovenia). In addition to the loss of some key fungicides for the control of STB since 2019, such as chlorothalonil, and the introduction of the QiI fenpicoxamid (Owen et al. 2017), significant changes have also occurred in the overall DMI landscape in Europe, with the revocation of epoxiconazole in 2020 and the approval for use in cereals of mefentrifluconazole in the same year (Strobel et al. 2020), with commercial approval dependent on the different member states. It is difficult to determine how this may have influenced the selection for CYP51-S524T, although sensitivity profiles of *Z. tritici* toward mefentrifluconazole and prothioconazole-desthio as presented by Heick et al. (2021) and recently by Kildea et al. (2024) suggests differences may exist. For example, the data presented by Kildea et al. (2024) demonstrated that, in addition to CYP51-S524T, overexpression of the efflux pump MFS1 (as reported by Omrane et al. (2017)) may be a significant contributor to DMI resistance, in particular toward mefentrifluconazole. Given the nature of the factors leading to this overexpression, specifically inserts in the promoter region, the screening of field samples as presented for the different target site alleles is likely to be more difficult. Even so, when such methods do become available, it will be possible to utilize the collections established as part of the present study and those of Hellin et al. (2021) to monitor how changes in this resistance mechanism has evolved in the wider European context.

Even though future research/monitoring is required to decipher which specific CYP51 haplotypes are associated with the increase of CYP51-S524T frequencies identified here, the fact that this alteration is on the rise indicates that the population is becoming less sensitive to the DMIs. Evidence from the EUROWHEAT trials network suggest that this is impacting the efficacy of some of the DMIs most relied upon, in particular prothioconazole (Jørgensen et al. 2022). Similarly, the increase in SDHC-N86S must equally be monitored. While there is no evidence from the EUROWHEAT network to suggest that the efficacy of the SDHIs has significantly decreased beyond the UK and Ireland, it is vital that strategies are put in place to limit the further spread of SDHI resistance. Utilizing agronomic practices in combination with varietal resistance can delay the onset of STB epidemics and hence reduce the need for intensive fungicide interventions. This is essential both to ensure reliable disease control continues to be achieved, but also to limit further selection for fungicide resistance.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s41348-024-01049-y.

**Acknowledgements** This project was conducted as part of the EURORES project established under the C-IPM ERANET, with financial assistance from each partner national funding body: Belgium (Moerman research fund, RESIST project at CRA-W), Denmark (Aarhus University, Department of Agroecology), Germany (Bavarian State Research Center for Agriculture), Ireland (Teagasc), Slovenia (Ministry of Agriculture, Forestry and Food; Slovenian Research and Innovation Agency (Programme P4-0431).

## Declarations

**Conflict of interest** The authors declare no conflicts of interest, and there were no animal of human subjects involved in the research.

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