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Meta-analysis of common wheat physiological response to biotic stresses

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Abstract

Common wheat (*Triticum aestivum* L.), like other plants, has evolved a variety of ways to resist pathogens. However, there are some studies that reported different results at the phenotypic and physiological levels. Therefore, this meta-analysis was conducted to reveal common trends, address some controversy, and a source of heterogeneity in 19 wheat phenotypic indices. It was found that the overall response is a reduction in thousand kernel weight (TKW), kernel number, plant biomass, grain yield, relative water content (RWC), soil and plant analysis development (SPAD), and proline, and an increase in ascorbate peroxidase (APX), catalase (CAT), glutathione-S-transferase (GST), hydrogen peroxide (H_2O_2), malondialdehyde (MDA), peroxidase (POX), polyphenol oxidase (PPO), superoxide dismutase (SOD), flavonoids, putrescine (PUT), salicylic acid (SA), and spermidine (SPD). However, the model was not significant for TKW, H_2O_2 , PUT, SA, and SPD ($p \geq 0.05$). The moderator analysis revealed that the effect of “cultivar” was significant on the kernel number ($p \leq 0.035$) and GST ($p \leq 0.008$), and the effect of “type of biotic stress” was significant on the grain yield ($p \leq 0.001$), APX ($p \leq 0.0001$), CAT ($p \leq 0.0009$), POX ($p \leq 0.0344$), flavonoids ($p \leq 0.001$), and SPAD ($p \leq 0.0201$). For plant biomass, the intercept effect of “cultivar” and “type of biotic stress” was significant ($p \leq 0.0187$).

The mixed-effect analysis addressed a source of heterogeneity in studies used in our study. However, to address additional factors affecting these parameters, some consideration for future studies is needed.

Keywords: antioxidant system, fungal diseases, heterogeneity, defense response, plant and pathogen interaction, *Triticum aestivum*.

Introduction

Among crops cultivated for producing food and feed, common wheat (*Triticum aestivum* L.) is one of the crucial crops that produce about 35% of the world's total food grain (>700 million tons) and 20% of calories and proteins. The importance of wheat even gets more value because an increase in the world population demands more food production, estimated to be 50% more food by 2050 (Miransari, Smith, 2019; Simón et al., 2021). One of the main constraints of sustainable food production is biotic stress (diseases and pests). It is estimated that pathogens and pests account for 21.5% of grain yield loss in wheat at a global level (Savary et al., 2019). As arable lands and natural sources are limited and even annually decrease, the strategy should be based on the yield increase (Simón et al., 2021). Breeding or genetic engineering of plants for stress tolerance has been one of the successful methods, especially in the case of tolerance to biotic stresses. However, these methods depend considerably on a comprehensive understanding of the crops' biological aspects involved in crop and biotic interaction. Moreover, studies have indicated that plant response to biotic stresses and their tolerance mechanism vary considerably and depend on many factors (Savary et al., 2019; Sun et al., 2020).

Many studies have examined the impact of biotic factors on physiological and biochemical traits. The common observation is that the growth parameters

such as dry weight, plant height, total biomass, root system, and fresh weight are mostly reduced by biotic factors, but the level of the reduction is different among plants (Veresoglou, Menexes, 2010; Simón et al., 2021). Plant response at physiological and biochemical levels are more specific. Indices related to chlorophylls, membrane integrity, reactive oxygen species (ROS), and antioxidant enzymes have been well studied, and it has been shown that plants employ various machinery to defend themselves against biotic stresses (Cvetkovska, Vanlerberghe, 2013; Sun et al., 2020; Iqbal et al., 2021). For example, superoxide dismutase (SOD) activity is significantly increased in many plants infected with pathogens (Simón et al., 2021), while some plants did not show a significant increase in their SOD activity (Cvetkovska, Vanlerberghe, 2013). Generally, defensive and adaptive response of plants to biotic factors encompass the coordinated alterations in physiological and biochemical traits at molecular and cellular levels. Mainly, the outcomes are a combination of reactions including strengthening of the cell wall to prevent the penetration of pathogens, triggering an efficient antioxidant system to scavenge ROS, inducing pathogen-related proteins (PR), and producing toxic secondary metabolites to prevent invasions (Sun et al., 2020). The challenge is to identify and understand a specific pattern of particular plant response to a wide variety of biotic stresses.

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A meta-analysis is a statistical approach to combining and synthesizing outcomes from multiple studies to attain a comprehensive understanding of a given problem and address questions. This approach has efficiently helped to address controversial results of different studies, identify sources of variations in results, and even to answer new questions about a particular problem in almost all disciplines (Gurevitch et al., 2018). Many studies have used meta-analysis and explored the response of plants to various biotic and abiotic factors. Yang et al. (2015) used a meta-analysis method to explore the differences in mycorrhizal fungi response between plants with different root systems. In another report (Pellegrino et al., 2015), a meta-analysis method has been used to show the response of wheat to arbuscular mycorrhizal fungi. Moreover, many studies use the meta-analysis to show wheat's response to stresses such as plant growth-promoting organisms (Pellegrino et al., 2015), ozone concentration (Feng et al., 2008), drought stress (Zhang et al., 2018), soil fertilizers (Wang et al., 2020), climate changes (Zhou et al., 2021), and many other reports (Veresoglou, Menexes, 2010; Yu et al., 2020). However, little effort has been given to understanding wheat response to biotic stresses, especially physiological and biochemical parameters such as plant biomass, pigments, and antioxidant systems.

This study collected and analysed outcomes of 272 samples for 19 phenotypic indices to explore the general response of wheat to various biotic stresses and address some controversial results. As plant response to the same stress varies considerably (Sun et al., 2020), this study provides reliable information to be used in engineering and screening tolerant cultivars of wheat. The results of our study will also quantify a cultivar type and type of biotic factors as the major source of heterogeneity across studies conducted about wheat and biotic stress interaction.

Material and methods

To search peer-reviewed publications via PubMed, Web of Science, and Google Scholar released before December 2020, the software Endnote (version X7.1) was used. The keywords used to search articles were "wheat diseases", "wheat pests", "biotic stress", "wheat response to biotic stress", "fungal diseases", "bacterial diseases", "wheat physiological response", "powdery mildew", "fusarium", and "Triticum aestivum". A total of 109 studies were selected based on the title, abstract, and keywords and then screened using the following criteria: 1) one or more common wheat (*Triticum aestivum* L.) cultivars were imposed to biotic stresses ($n = 78$); 2) only original and research articles were selected ($n = 39$); 3) control and treated groups were studied using an appropriate experimental method ($n = 33$); 4) the sample size, means, and standard deviation (SD) or standard error (SE) could be extracted from the text, table, or graphs using the software WebPlotDigitizer (Rohatgi, 2017) for control and biotic stress-affected groups ($n = 21$); 5) at least one of growth parameters or physiological indices was included in the study ($n = 21$).

After screening, 21 studies were selected to extract data for meta-analysis. In studies with more than one cultivar or biotic type and treatments with more than one level, each treatment was considered as an individual observation. A total of 272 observations for 19 growth parameters and physiological indices was extracted and used in the meta-analysis. The phenotypic indices were thousand kernel weight (TKW) (g), kernel number (n), plant biomass (g), grain yield (kg ha^{-1}), activity of ascorbate peroxidase (APX) (unit mg^{-1} protein), catalase (CAT) (unit mg^{-1} protein), and glutathione-S-transferase (GST) (unit mg^{-1} protein), hydrogen peroxide (H_2O_2) ($\mu\text{g g}^{-1}$ FW), malondialdehyde (MDA) (nmol g^{-1} FW), activity of peroxidase (POX) (unit mg^{-1} protein), polyphenol oxidase (PPO) (unit mg^{-1} protein), and superoxide dismutase (SOD) (unit mg^{-1} protein), flavonoids (mg g^{-1}),

relative water content (RWC) (%), soil and plant analysis development (SPAD), proline ($\mu\text{M g}^{-1}$ FW), putrescine (PUT) (nmol g^{-1} FW), salicylic acid (SA) (nmol g^{-1} FW), and spermidine (SPD) (nmol g^{-1} FW).

To estimate response ratios (lnRR) as effect sizes (Moeller, 2006) and meta-analysis, the R package metafor (Viechtbauer, 2010) was used. To calculate the log, means, SD, and sample sizes of control and biotic stress-affected groups were used. The effect size estimates the magnitude of the treatment effect. The lnRR was calculated as $\ln(X_c/X_t) = \ln X_c - \ln X_t$, where X_c and X_t are the mean values for control and biotic stress-affected groups. As phenotypic indices were from different studies that reported results in different units, this study used SD (Worchel et al., 2013). To convert SE to SD when SE was reported and SD was not provided, the equation $\text{SD} = \text{SE} \times (n)^{1/2}$ was used. The calculated effect sizes were weighted using $\ln[(1/n_c) \times (S_c/X_c)^2 + (1/n_t) \times (S_t/X_t)^2]$ known as the Hedges estimator (Hedges, Olkin, 1985), where S_c and S_t represent the SD with n_c and n_t as sample sizes of biotic stress-affected and control groups, respectively.

To conduct the meta-analysis, a mixed-effect model was used in this study. Studies included in this meta-analysis are not identical in their methods and conditions, so this could introduce variability to the actual effects of treatments. The mixed-effect model counters variability as purely random. The random-effect model is $\theta_i = \mu + u_i$, where $u_i \sim N(0, \tau^2)$ calculates variability using τ^2 (the estimated amount of residual heterogeneity). The statistical significance of moderators and the amount of heterogeneity were tested by the Q_M test and R^2 , respectively. When heterogeneity was significant, the cultivar in two levels (resistant or susceptible) and the type of biotic factor in 13 levels: barley yellow dwarf virus (BYDV), *Fusarium culmorum*, *F. graminearum*, *F. oxysporum*, *Magnaportheorhizae*, powdery mildew, *Puccinia graminis*, *P. striiformis*, *P. triticea*, soil-borne wheat mosaic virus (SBWMV), Triticum mosaic virus (TriMV), wheat dwarf virus (WDV), and wheat streak mosaic virus (WSMV), were used as a moderator. The use of moderators is a recommended practice when there is a possibility of high heterogeneity (Viechtbauer, 2010).

Results

In this study, almost all previous studies that report the impact of biotic stresses on wheat physiological parameters were surveyed (109 studies). Table 1 shows the summarised results of the search and the studies that were included in the present study. The literature review indicated that little attention has been taken to physiological traits. Most of the studies (96.06%) reported genome-wide, genetic engineering, proteomics, and transcriptomic aspects. The studies selected for the meta-analysis included 99 cultivars and 18 biotic factors.

The statistical analysis of estimates using p -value showed that the biotic factors did not affect wheat TKW, H_2O_2 , PUT, SA, and SPD ($p = 0.05$) (Table 2). The results for kernel number, plant biomass, APX, CAT, and PPO ($p \leq 0.001$), grain yield, RWC, proline, and POX ($p \leq 0.01$), and for GST, MDA, SOD, and flavonoids ($p \leq 0.05$) were significant with 95% CI (confidence interval). The growth parameters decreased significantly under the biotic stress conditions. For instance, the kernel number, plant biomass, and grain yield decreased by 39.08%, 41.92%, and 8.03%, respectively in the biotic stress-affected plants compared to the mean value of the control groups. The results of pigment indices showed a significant decrease of soil and plant analysis development (SPAD) by 11.21% and an increase of total flavonoids by 3.43% in the control groups. In the biotic stress-affected groups, the meta-analysis of phenotypic indices related to the components of the antioxidant system showed a significant increase in MDA by 21.06%, APX by 38.12%, CAT by 41.07%, GST by 36.71%, POX by 25.48%, PPO by 58.43%, and SOD by 36.12% (Figure 1).

The heterogeneity analysis indicated a considerable heterogeneity ($I^2 = 93.90\%$, $p \leq 0.0002$) for all

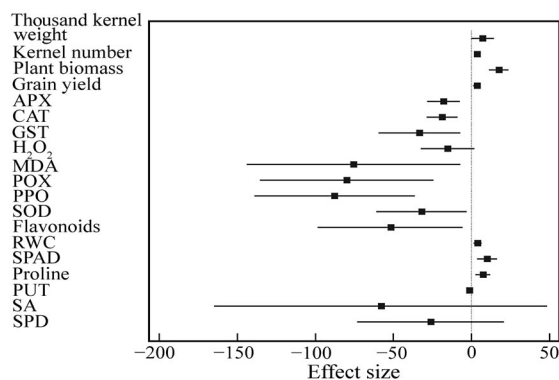
Table 1. The summarised results of the search and the studies that were included in the present study

| | |
|---|------|
| Total search | 3482 |
| Exclude keywords: proteomics, genome-wide, transcriptome, transcriptomics, and genetics | 137 |
| With the exact phrases “wheat, growth, and physiological” | 109 |

Table 2. Summary of biotic stress effects on wheat physiological response

| Parameter | K | Estimate | SE | z-value | p-value | ci.lb | ci.ub | Significance |
|--|----|----------|----------|---------|---------|----------|----------|--------------|
| Thousand kernel weight | 22 | 7.2774 | 3.7356 | 1.9481 | 0.0514 | -0.0442 | 14.599 | ns |
| Kernel number | 17 | 3.8361 | 0.821 | 4.6723 | ≤0.0001 | 2.2269 | 5.4453 | *** |
| Plant biomass | 20 | 17.5922 | 3.1526 | 5.5803 | ≤0.0001 | 11.4133 | 23.7712 | *** |
| Grain yield | 15 | 3.6211 | 1.3118 | 2.7604 | 0.0058 | 1.0501 | 6.1922 | ** |
| Ascorbate peroxidase (APX) | 18 | -17.7955 | 5.3051 | -3.3544 | 0.0008 | -28.1933 | -7.3978 | *** |
| Catalase (CAT) | 32 | -18.7107 | 5.0535 | -3.7026 | 0.0002 | -28.6153 | -8.8061 | *** |
| Glutathione-S-transferase (GST) | 14 | -334.203 | 134.7713 | -2.4798 | 0.0131 | -598.35 | -70.0562 | * |
| Hydrogen peroxide (H ₂ O ₂) | 10 | -157.164 | 86.271 | -1.8217 | 0.0685 | -326.252 | 11.9241 | ns |
| Malondialdehyde (MDA) | 14 | -75.4506 | 34.9036 | -2.1617 | 0.0306 | -143.86 | -7.0408 | * |
| Peroxidase (POX) | 19 | -79.8056 | 28.356 | -2.8144 | 0.0049 | -135.382 | -24.2289 | ** |
| Polyphenol oxidase (PPO) | 16 | -87.5567 | 26.1706 | -3.3456 | 0.0008 | -138.85 | -36.2632 | *** |
| Superoxide dismutase (SOD) | 12 | -31.883 | 14.7442 | -2.1624 | 0.0306 | -60.7811 | -2.985 | * |
| Flavonoids | 34 | -517.473 | 237.235 | -2.1813 | 0.0292 | -982.445 | -52.5005 | * |
| Relative water content (RWC) | 5 | 4.0023 | 1.2834 | 3.1186 | 0.618 | 1.487 | 6.5176 | ** |
| SPAD | 10 | 10.2177 | 3.257 | 3.1371 | 0.0017 | 3.834 | 16.6014 | ** |
| Proline | 4 | 7.3808 | 2.5064 | 2.9447 | 0.0737 | 2.4683 | 12.2933 | ** |
| Putrescine (PUT) | 3 | -1.3105 | 0.8809 | -1.4877 | 0.1368 | -3.0371 | 0.416 | ns |
| Salicylic acid (SA) | 4 | -5799.61 | 5440.489 | -1.066 | 0.2864 | -16462.8 | 4863.551 | ns |
| Spermidine (SPD) | 3 | -26.0369 | 23.9616 | -1.0866 | 0.2772 | -73.0008 | 20.927 | ns |

K – number of observations; Estimate – the magnitude of the treatment effect calculated as $\ln RR = \ln(X_i/X_c) = \ln X_i - \ln X_c$; SE – the standard error of the predicted values; ci.lb (lower bound of CI) and ci.ub (upper bound of CI) of the corresponding 95% CI; ns – not significant ($p > 0.05$); *, **, *** – $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$.



Note. Filled squares represent the weighted effect for the mean values of wheat response; horizontal bars indicate a 95% CI; values on the right side of the dashed line (positive values) mean that the values are more common in the control groups, and the left side of the line (negative values) means that the values are more common in the biotic stress-affected groups.

Figure 1. Response of wheat growth parameters and physiological indices to biotic stress

parameters. Thus, to reduce the heterogeneity, the mixed-effect model and “cultivar” and “type of biotic factors” were used as moderators. The test of the moderators for “cultivar” was significant for kernel number, plant biomass, and GST. For “type of biotic factors”, the test was significant for plant biomass, grain yield, APX, CAT, POX, flavonoids, and SPAD (Table 3).

Furthermore, the moderator test for nonsignificant parameters (“cultivar” and “type of biotic stress”) was performed based on the “study” as a source of heterogeneity. The result was significant for MDA ($Q_M = 94.5616$; $p \leq 0.001$), SOD ($Q_M = 9.5978$; $p \leq 0.0082$), and PPO ($Q_M = 269.5362$; $p \leq 0.008$). As represented in Figure 2, when moderators were not used in the model, all observations lay outside the triangular region. When the

cultivar types or the type of biotic stress were used as a moderator, observations lay inside the triangular region.

Discussion

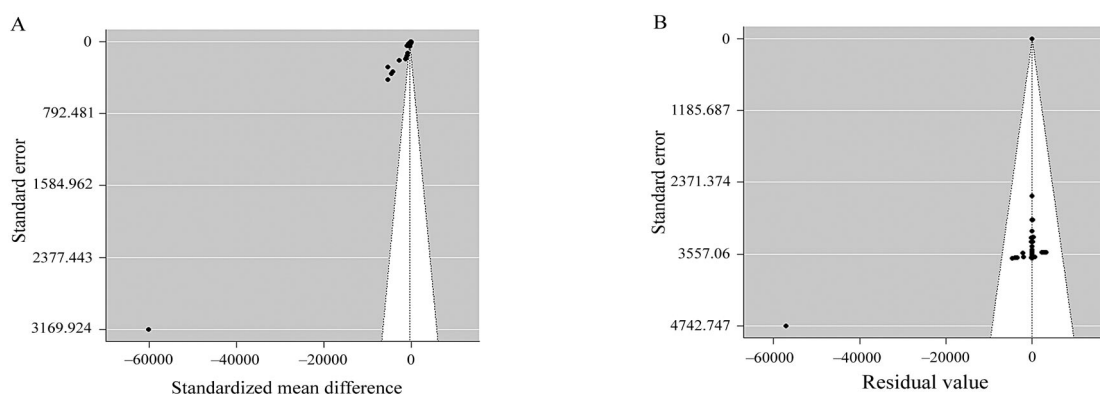
Studies on wheat growth parameters and physiological indices have shown that biotic stresses such as fungi, pests, viruses, and bacteria reduce plant growth (plant biomass, kernel number, grain yield, root dry weight, stem dry weight, plant height, etc.) and reduce or increase physiological parameters (chlorophyll content, antioxidant enzymes, osmolytes, amines, etc.) (Chen et al., 2007; Pál et al., 2013; Nygren et al., 2015; Khaledi et al., 2016; 2017; Sorahinobar et al., 2016; Mohapatra, Mitra, 2017; Khaled et al., 2018; Choudhury et al., 2019; Kroese et al., 2020; Nancarrow et al., 2021). Most researchers concluded that resistant cultivars showed less reduction in their growth parameters (Nygren et al., 2015; Sorahinobar et al., 2016; Khaled et al., 2018; Wang et al., 2020; Simón et al., 2021). Moreover, many reports showed that the antioxidant system was more efficient in biotic stress-resistant cultivars compared to susceptible cultivars (Chen et al., 2007; Cvetkovska, Vanlerberghe, 2013; Khaledi et al., 2016; Iqbal et al., 2021). This efficiency was mainly reported in two ways: (1) a high level of antioxidant enzyme activity, mostly CAT and SOD; (2) an early accumulation of reactive oxygen species (ROS) and induction of antioxidant enzymes (Pál et al., 2013; Khaledi et al., 2017; Khaled et al., 2018).

However, there are some points that could not be interpreted from individual studies. For example, it was reported that GST and APX activity in resistant cultivars in the early days after infection was higher than in susceptible cultivars; however, other reports showed a high level of activity for GST in the early days but not for APX in resistant cultivars. Moreover, many studies have focused on the response of wheat to particular biotic factors, whereas wheat is facing multiple types of biotic stresses in the environment. To gain a comprehensive

Table 3. Heterogeneity analysis for the subgroup analysis of 12 significant parameters with two moderators (“cultivar” and “type of biotic stress”)

| Parameters | Q_M | p -value | R^2 % | Cultivar | Type of biotic stress |
|---------------|----------|---------------|---------|----------|--|
| Kernel number | 210.7135 | ≤ 0.035 | 93.47 | R, S | ns |
| Plant biomass | 15.2070 | ≤ 0.0187 | 88.52 | R, S | BYDV SBWMV |
| Grain yield | 69.5978 | ≤ 0.001 | 92.24 | ns | BYDV <i>Puccinia triticina</i> <i>Fusarium graminearum</i> |
| APX | 159.0982 | ≤ 0.0001 | 87.12 | ns | <i>Fusarium oxysporum</i> Powdery mildew <i>Fusarium graminearum</i> |
| CAT | 26.3644 | ≤ 0.0009 | 38.16 | ns | Powdery mildew <i>Puccinia triticina</i> |
| GST | 210.7135 | ≤ 0.008 | 99.54 | R, S | ns |
| MDA | 1.5297 | $= 0.8214$ | 8.37 | ns | ns |
| POX | 12.0257 | ≤ 0.0344 | 31.01 | ns | <i>Puccinia triticina</i> |
| PPO | 5.5753 | $= 0.2332$ | 14.26 | ns | ns |
| SOD | 7.2057 | $= 0.655$ | 31.28 | ns | ns |
| Flavonoids | 21.1924 | ≤ 0.001 | 39.62 | ns | <i>Fusarium graminearum</i> |
| SPAD | 9.8285 | ≤ 0.0201 | 47.63 | ns | TriMV |

Explanation of parameters in Table 2; Q_M – test of moderators; R^2 – the amount of heterogeneity accounted for cultivar: R stands for “resistant” and S for “susceptible”; ns – not significant ($p > 0.05$); BYDV – barley yellow dwarf virus, SBWMV – soil-borne wheat mosaic virus, TriMV – Triticum mosaic virus.



Note. The white triangle indicates the observations in the absence of bias and heterogeneity; the R package metafor was used for the meta-analysis and to calculate the standard error, standardized mean difference, and residual value.

Figure 2. Illustration of a funnel plot for the model without a moderator (A), and with “cultivar” and “type of biotic stress” as moderators (B)

understanding and address some controversies in reports, this study used the meta-analysis method based on the mixed-effect model. To investigate the physiological indices of the wheat response to biotic factors, address a source of heterogeneity among studies, and gain new insight into wheat and biotic stress interaction, we synthesized the results of different studies.

Wheat kernel number, TKW, biomass, grain yield, and RWC are reduced by biotic stresses, and the level of reduction depends on the tolerance of the cultivar, stage of infection, and the type of biotic factors (Mohapatra, Mitra, 2017; Choudhury et al., 2019; Kroese et al., 2020; Nancarrow et al., 2021). The results of our study showed a significant reduction of these parameters except for TKW, which was not significant (Table 2, Figure 1). The level of reduction for these parameters is different across studies. The meta-analysis showed that the plant biomass was negatively influenced by biotic factors more than the kernel number and yield. The mixed-effect model analysis by two moderators (“cultivar” and “type of biotic stress”) showed that the kernel number is significantly changed (93.47%) by cultivar type. It was found that the cultivar type is a significant heterogeneity source for the kernel number. This observation might come from using a few pathogens infecting aerial parts of wheat in the studies included in our meta-analysis. However, 88.52% of plant biomass was changed by the cultivar type and type of biotic stress. Resistant cultivars have more plant biomass in normal and infected states compared to susceptible ones.

The results of the current study showed that among 13 biotic factors, BYDV and SBWMV had a significant part in reducing plant biomass. For yield, 92.24% of alteration is significantly based on changes in biotic factors, and BYDV showed a significantly negative moderator effect on grain yield (Table 3). BYDV and SBWMV are viral diseases with a high occurrence rate worldwide, and it has been reported that an average of 38% grain yield loss could rise to 80% in early infections (Aradottir, Crespo-Herrera, 2021). The results of our study emphasise the importance of studying wheat and virus interaction and the need to develop efficient ways for managing viral diseases.

MDA is a product of the peroxidation processes in membrane lipids (Morales, Munné-Bosch, 2019), and in our meta-analysis, the change of MDA is used to represent the level of the damage caused by oxidative stress. However, some studies suggested that MDA in association with the ROS scavenging system could act as a protector to limit the damage to proteins, and a signal to the molecular defense machinery (Schmid-Siegert et al., 2016; Morales, Munné-Bosch, 2019). It has been shown that the MDA importance as a damager or protector depends on aldehyde dehydrogenases (ALDHs), the enzymes that are induced by H_2O_2 (Zhao et al., 2018; Morales, Munné-Bosch, 2019). The results of our study revealed that H_2O_2 and MDA levels are high in infected plants; however, the results for H_2O_2 were not significant. Moreover, 92% of MDA variability depends on the “study” moderator. Similarly, SOD and PPO were significantly high in infected groups, but two

moderators (“cultivar” and “type of biotic stress”) used in this study contributed only 31% and 14% as sources of heterogeneity (Table 3). It means that these parameters should be interpreted with caution. This may be due to differences in the methodologies, infection intensity, the plant growth stage, tissue, or other factors. To evaluate the effects of other moderators on these parameters, further research and a larger number of studies are required.

The meta-analysis revealed the factors affecting the pattern of APX, CAT, GST, and POX in the wheat response to biotic stresses. In general, APX, CAT, GST, and POX levels are increased in wheat infected with pathogens, and their activity is high in resistant cultivars compared to that of sensitive ones (Pál et al., 2013; Khaledi et al., 2016; Khaled et al., 2018). In this study, the meta-analysis showed the same results, and these enzyme activities were significantly high in infected groups and comparatively more expressed in resistant plants under infection conditions. POX activity was prominent compared to APX, CAT, and GST (Figure 1). The result of the mixed-effect model with two moderators was interesting. The effect size of biotic factors (*Fusarium graminearum*, *F. oxysporum*, powdery mildew, and *Puccinia triticina*) on the activity of APX (87.12%), CAT (38.16%), and POX (31.01%), respectively was significant, while the cultivar type (resistant or susceptible) showed no significant effect (Table 3). On the other hand, the effect size of the cultivar type was strongly significant for GST (99.54%).

Some studies showed that the changes in SPAD were non-significant, while most studies reported that biotic factors reduced SPAD in infected plants. The meta-analysis indicated that a common trend for SPAD was the reduction in response to biotic factors. Similar to SPAD, reports about flavonoids are controversial. The results of this study showed that the infected plants commonly increased their flavonoid content (Tables 2 and 3). Overall, the amount of flavonoids is believed to increase during plant and pathogen interaction (Wallis, Galarneau, 2020). In our study, the use of moderators revealed that 47.63% of changes in SPAD were a result of TriMV infection across 18 pathogens evaluated here.

Our study revealed a higher proline content in the control plants and higher SA and SPD in the infected plants (Figure 1). However, the model results were not significant for SA and SPD (Table 2). The results showed a non-significant effect of biotic factors on TKW and H_2O_2 . The small number of studies with relatively equal effect sizes could be the contributors to non-significance results for TKW, H_2O_2 , PU, SA, and SPD. So, there is a need for more data to have a reliable interpretation of these parameters. In contrast to the obtained results, previous studies (Gupta et al., 2020) demonstrated that these parameters significantly changed in plants imposed to biotic stress.

This meta-analysis revealed that there was considerable heterogeneity among studies (Figure 2). Using moderators, a source of heterogeneity for several parameters was indicated (Table 3). However, further studies considering other factors such as the growth stage, infection time, infection duration, disease intensity, and plant tissue are essential to address this heterogeneity source. This study could not address these factors, because there was no or a small quantity of available data, and in the case of tissue, most studies reported the same tissue. The results of our research could address some controversy among studies, especially for antioxidant enzymes. Moreover, it was found that the cultivar type and type of biotic stress have profound effects on the kernel number, plant biomass, grain yield, APX, and GST. The moderators accounted for 30% to 40% of the variation for CAT, POX, flavonoids, and SPAD in the wheat response to biotic stress. The results of MDA, PPO, and SOD should be taken carefully, as there is a possibility for exciting bias in data and considerable effects of non-related factors on the outcomes.

Conclusion

The performed meta-analysis confirmed that 19 wheat phenotypic indices were reduced as a result of response to biotic factors, especially viruses causing a substantial decrease in wheat biomass and grain yield. Moreover, the results of our study addressed some controversy in physiological parameters and high heterogeneity. In this effort to analyse the wheat response to biotic factors, three major gaps in studies were identified: (i) as long as we know, there were no studies that explore the wheat response to a combination of biotic factors; (ii) a cultivar type and type of biotic factors addressed a considerable part of heterogeneity across studies, but still, there are many factors that should be considered in the future studies; (iii) to have a comprehensive understanding about wheat under biotic stresses, future studies must use a consistent manner and design to conduct and share data.

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Paprastųjų kviečių augimo metaanalizė ir fiziologinis atsakas į biotinį stresą

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Santrauka

Paprastųjų kviečių, kaip ir kitų augalų, atsparumas patogenams skiriasi. Įvairiuose oksliniuose tyrimuose pateikiami fenotipinių ir fiziologinių rodiklių duomenys nesutampa, todėl ši metaanalizė atlikta siekiant atskleisti vyraujančias tendencijas, išanalizuoti probleminius klausimus ir nustatyti kviečių 19 fenotipinių rodiklių heterogeniškumo šaltinį. Nustatyta, kad bendras atsakas yra tūkstančio grūdų svorio, grūdų skaičiaus, augalų biomasės, grūdų derliaus, santykinio vandens kiekio, chlorofilo, išreikšto SPAD (angl. *soil and plant analysis development*) vienetais, ir prolinio sumažėjimas ir askorbato peroksidazės, katalazės, glutationo-S-transferazės, vandenilio peroksido, malondialdehido, peroksidazės, polifenolio oksidazės, superoksido dismutazės, flavonoidų, putrescino, salicilo rūgšties bei spermidino kiekio padidėjimas. Tačiau modelio taikymas neturėjo didelės reikšmės tūkstančio grūdų svorio, vandenilio peroksido, putrescino, salicilo rūgšties ir spermidino rodikliams ($p \leq 0,05$). Moderatoriaus analizė parodė didelę rodiklio „veislė“ įtaką grūdų skaičiui ($p \leq 0,035$) ir glutationo-S-transferazės kiekiui ($p \leq 0,008$), taip pat reikšmingą rodiklio „biotinis stresas“ įtaką grūdų derliui ($p \leq 0,001$), askorbato peroksidazės ($p \leq 0,0001$), katalazės ($p \leq 0,0009$), peroksidazės ($p \leq 0,0,344$) bei flavonoidų kiekiui ($p \leq 0,001$) ir SPAD ($p \leq 0,0201$). Rodiklių „veislė“ ir „biotinis stresas“ ribojantis poveikis augalų biomasei buvo reikšmingas ($p \leq 0,0187$).

Eksperimento metu taikant kompleksinio poveikio analizę nustatytas heterogeniškumo šaltinis, tačiau reikėtų papildomų šiuos rodiklius veikiančių faktorių tyrimų.

Reikšminiai žodžiai: antioksidacinė sistema, grybelinės ligos, heterogeniškumas, apsauginės reakcijos, augalų ir patogenų sąveika, *Triticum aestivum*.