



# Fusarium species causing head blight in wheat and barley show no vertical races

Nachaat Sakr

Department of Agriculture, Atomic Energy Commission of Syria, Damascus, (AECS)

Corresponding author e-mail: [ascientific@aec.org.sy](mailto:ascientific@aec.org.sy)

## Abstract

On a global scale, *Fusarium* head blight (FHB) is one of the most noxious diseases of wheat and barley. One or two *Fusarium* species out of 17 pathogens implicated in the complex FHB disease do not have vertical races following infection in bread wheat; however, no reports support this observation in durum wheat and barley. To end this, 16 fungal isolates of varying aggressiveness of four *Fusarium* species were tested on eight bread and durum wheat and barley cultivars covering a wide range from moderate resistance to susceptibility. Nine pathogenic components obtained under *in vitro*, growth chamber and field conditions were measured to determine whether true vertical races exist within the four tested *Fusarium* species. Although combined analysis of bio-experiments showed that isolate  $\times$  cultivar interactions were significant, this relationship was unstable over experiments. However, the tested three bread wheat, three durum wheat and two barley cultivars showed consistent resistance to fungal isolates within each tested species, showing that *F. culmorum*, *F. solani*, *F. verticillioides*, and *F. equiseti* do not have vertical races. Our data concluded that the resistance to FHB in wheat and barley was of the horizontal and non-species specific type. There was no signal for any vertical genes in all tested *Fusarium* species. Consequently, the resistance genes in sources presently employed in breeding programs are not expected to succumb to new FHB races in the near future. To our best knowledge, this is the first report to show the absence of vertical *Fusarium* races upon infection durum wheat and barley, and is harmony with earlier reports conducted with bread wheat infected with *F. graminearum* and *F. culmorum*.

**Keywords:** cultivar-by-isolate interaction, FHB resistance, resistance breeding, host-specificity.

## 1. Introduction

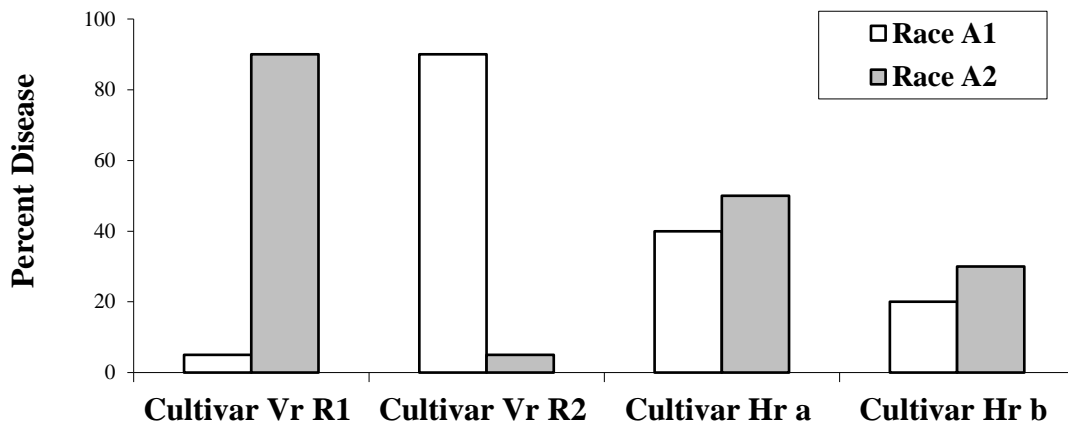
Wheat, comprising bread (*Triticum aestivum*) and durum (*T. durum*), is a worldwide crop of main nutritional importance and economic value, as it supplies 20% of the protein and calories consumed by the globe's population [1]. Barley (*Hordeum vulgare*) is one of the oldest planted grain crops ranking fourth in importance, among small-grain cereals, and successfully grown under a diverse range of environments [1]. Almost 80%–90% of *H. vulgare* kernel yield is assigned for livestock feed, while the remaining 10% is transformed into malt and distilling for brewing, and baking.

From an economic point of view, their importance emerges from being widely used for food and feed production in all parts of the world. Every year, they are cultivated in an area of 270 million ha and producing over 905 million metric tons [1]. Although the wheat and barley kernel production has continued to augment over the last 50 years, their yields are challenged by several fungal diseases [2], but *Fusarium* head blight (FHB) is one of the most destructive diseases in many regions worldwide [3]. FHB not only provokes important production losses but also decreases the quality of harvested kernels due the contamination of

mycotoxins, such as the trichothecene deoxynivalenol (DON), released during FHB infection and colonization. Consuming of mycotoxin-contaminated kernels and their products leads to chronic or acute health hazards to human and livestock. Taken into consideration its toxicity, DON allowance is regulated in several countries [4]. Economic losses resulted from FHB in wheat and barely have been over \$ 4.8 billions since 1990 in USA [5].

In the plant pathology literature, in many fungus-host relationships two resistance types cooperatively exist [6] as shown in Figure (1). Qualitative resistance, i.e., vertical resistance,

interacted with the qualitative component of pathogenicity, i.e., virulence, is obviously race-specific. This race specificity has been elucidated by supposing a gene-for-gene relationship that provides a near- absolute protection to disease [7] (Figure 1). Quantitative resistance, i.e., horizontal resistance, interacting with aggressiveness (i.e., the ability of a pathogen isolate to cause disease on a susceptible host) and linking with the existence of quantitative trait loci, QTLs, does not confer complete protection [8], but is proven to be efficient against all known isolates of the pathogen [9] (Figure 1).



**Figure 1.** Plot of percent disease in two cultivars with vertical resistance, i.e., qualitative resistance, (Vr R1 with resistance gene R1; Vr R2 with resistance gene R2) and two cultivars lacking vertical resistance (R genes) but showing some horizontal resistance, i.e., quantitative resistance, (Hr a, Hr b) infected with two pathogen races (A1 with avirulence against R1; A2 with avirulence against R2). Vertical resistance presents a strong interaction with the races (i.e. is 'race-specific'). Horizontal resistance does not (i.e. is 'non-race-specific') although it shows significant and main effects of Cultivar (cultivar Hr a is more susceptible to both races than Hr b) and Race (race A2 is more aggressive than A1 on both cultivars, and this is also evident in the vertically resistant cultivars where the R gene is ineffective) as shown by Keane [6]

Indeed, Van der Plank [10] postulated that the quantitative resistance genes are equally efficient for all pathogen isolates. The mechanisms of wheat and barley resistance to head blight disease are very complicated, and now it is commonly agreed that *Fusarium* resistance is controlled by a polygenic interaction. It is, however, important that several reports showed durable and common resistance to diverse *Fusarium* pathogens causing FHB [11]. In this paper, we used the aggressiveness term for the disease-causing ability of the given isolate, as virulence is taken

for the race-specific pathogens like rusts [10]. The employment of quantitatively resistant wheat and barley cultivars is a main component of a sustainable control policy of FHB [4].

A number of pathogens of *Fusarium* may be responsible, but mostly *F. graminearum* and *F. culmorum* predominate as the causative agent for FHB [12]. Nevertheless, the less repeatedly species have also been isolates from wheat and barley fields globally such as *F. cerealis*, *F. equiseti* and *F. poae*, and, to a lesser extent, *F. solani*, *F. verticillioides* and *F. oxysporum* [5]. Isolate variation for aggressiveness and DON

production has been well established in *Fusarium* pathogens [13, 14]. *F. culmorum* and *F. graminearum* are non-host specific, i.e. they are pathogenic to wheat, barley, maize and other cereals and grasses without exhibiting specialization for any one crop [5, 12, 14]. However, some host preferences among *Fusarium* pathogens have been reported [15]. The possibility that resistance to head blight in wheat and barley may be race-specific has been the subject of debate. Tekauz *et al.* [16] identified two physiological forms of *F. avenaceum* and three of *F. culmorum* and *F. graminearum* and on the basis of their aggressiveness to eight different cultivars of wheat. Snijders [17] divided isolates of *F. culmorum* into three aggressiveness groups and inoculated 18 wheat cultivars, from which he distinguished seven isolates that he claimed presented race-specific genes. No confirmation has been established for the presence of races of *F. graminearum* or *F. culmorum* adapted to different wheat cultivars [11, 12]. To what extent resistance to *F. graminearum* is related to resistance to *F. culmorum* is not evident. Mesterhazy [18, 19] observed correlation coefficients of up to 0.90 between the response of wheat cultivars to *F. culmorum* isolates and their reaction to *F. graminearum* isolates. Spring wheat cultivars which had been found to be resistant to FHB caused by *F. graminearum* were also resistant to *F. culmorum* [20]. Miedaner *et al.* [21] observed for 16 rye inbred cultivars that the genetic basis of resistance to FHB caused by the two *Fusarium* pathogens is very likely the same. In addition, Arseniuk *et al.* [15] reported that the cereal resistance to a wide range of *Fusarium* species encompassing the above two should be taken into account at the genus and not at the species level. At present, there is no strong verification for race-specific resistance in wheat to any of the FHB pathogens [3, 4, 5].

It is clear now that *F. culmorum* and *F. graminearum* do not have vertical races and the resistance is race-non-specific [22]. However, no studies support this observation in durum wheat and barley. In this investigation, we hypothesized that if the tested three bread wheat, three durum wheat and two barley cultivars covering a wide range from moderate resistance to susceptibility show a consistent resistance to fungal isolates of varying

aggressiveness within each tested species, it means that *F. culmorum*, *F. solani*, *F. verticillioides*, and *F. equiseti* which are the prevailing species infecting wheat in Syria [23] do not have vertical races. This research was initiated to evaluate the (non-)specificity of FHB resistance in small grain cereals, i.e., wheat and barley, for *Fusarium* species and for isolates within them. In this present report, our aim was to detect whether true vertical races exist within four *Fusarium* species upon artificial infection on a set of diverse bread wheat, durum wheat and barley under several experimental conditions.

## 2. Materials and method

### 2.1. Wheat and barley cultivars

All cultivars were winter type wheat and barley. Eight bread wheat, durum wheat and barley cultivars differing in their reactions to artificial infection with FHB pathogens were selected on the basis of the results of previous experiments, i.e., *in vitro*, growth chamber and field conditions [23]. The wheat and barley cultivars Arabi Aswad (AS) and Bohoth10 (bread) could be characterized as moderately resistant, Arabi Abiad (AB), Cham4 and Douma4 (bread) as moderately susceptible, Cham7 and Cham9 (durum) as susceptible to moderately susceptible and Acsad65 (durum) as susceptible to FHB.

### 2.2. Fungal isolates

*Fusarium* isolates, derived from monoconidial cultures, were obtained from wheat head samples, collected through the 2015 growth season in nine districts in Ghab Plain with a FHB history, one of the principal Syrian wheat production areas. This analysis is based on 16 *Fusarium* isolates (4 *F. culmorum*, 6 *F. solani*, 4 *F. verticillioides* (synonym *F. moniliforme*) and 1 *F. equiseti*). The basic criteria for selection of isolates were the results of aggressiveness studies under previous several experimental conditions. By using the keys of Leslie and Summerell [24], single spore cultures on Petri-dishes with potato dextrose agar (PDA, HiMedia, HiMedia Laboratories) with 13 mg/l kanamycin sulphate (C<sub>18</sub>H<sub>38</sub>N<sub>4</sub>O<sub>15</sub>S) added after autoclaving at 121°C (Systec, 3870 EL), were classified morphologically to species level. By using

random amplified polymorphic DNA markers (Operon Technologies), the 16 *Fusarium* species causing head blight isolates were recently analyzed [23]. The isolates were preserved by freezing at -16°C or in sterile distilled water at 4°C till use [25].

### 2.3. Inoculum preparation

FHB inoculum used for inoculation for the *in vitro*, growth chamber and field trials was normally performed as following: fungal suspension or four to six agar plugs out of each stored single-spore culture were put over the surface of Petri dishes PDA and incubated in an incubator (JSPC, JS Research Inc.) under continuous darkness at 22°C for 10 days to allow sporulation and fungal development. Following incubation, isolates were covered with 10 ml of sterile distilled water and conidia were dislodged. Fungal suspensions were filtered through 2 layers of sterile cheesecloth to remove the pieces of mycelia and agar and directly quantified with a Neubauer chamber under an optical microscope and diluted to a desirable concentration ( $1 \times 10^6$  spores per ml for *in vitro* experiments and  $5 \times 10^4$  spores per ml for *in planta* experiments) as inoculum sources.

### 2.4. Identification of criteria to detect the presence of vertical races in FHB pathogens

The general methodology selected to answer the question on the existence of vertical races is an extension of an approach developed earlier towards the same problem in van Eeuwijk *et al.* [27]. True vertical races do not exist within the four tested species if isolate  $\times$  cultivar interactions was unstable over experiments and if the tested three bread wheat, three durum wheat and two barley cultivars covering a wide range from moderate resistance to susceptibility present a consistent resistance to fungal isolates of varying aggressiveness within each tested species. In order to test whether true vertical races exist within the four tested species, nine pathogenic responses at the seedling and adult plant stages under *in vitro*, climatic growth chamber and field conditions of three bread cultivars, three durum cultivars and two barley cultivars with varying resistance levels to head blight to four *Fusarium* species was evaluated. Pathogenic reactions of all cultivars infected with *Fusarium* fungi were previously evaluated according to methods described by Sakr [23]:

latent period (LP) of detached leaf inoculation, area under disease progress curve (AUDPC) of Petri-dish inoculation and coleoptile dwarfing (CD) of a coleoptile infection detected *in vitro*, disease incidence (DI, Type I) and disease severity (DS, Type II) detected using a detached head test (DHT) under controlled conditions, disease incidence (DI<sup>CC</sup>, Type I) detected using a head artificial inoculation and disease severity (DS<sup>CC</sup>, Type II) detected using a floret artificial inoculation under controlled conditions in a growth chamber, and disease incidence (DI<sup>FC</sup>, Type I) and disease severity (DS<sup>FC</sup>, Type II) detected using a head artificial inoculation under field conditions (FC) over the three growing seasons. Since no significant interaction year  $\times$  fungus/cultivar was observed (climatic data for the station were somewhat similar during the three growing seasons [23]), field data were shown as the averages of the three growing seasons.

### 2.4. Statistical analyses

The experimental data were subjected to analysis of variances (ANOVA) using DSAASTAT add-in version 2011. Before statistical analysis, the percentages were transformed using the angular transformation to stabilize variances. ANOVA incorporating the Fisher's LSD test at  $P < 0.05$  was used to compare the means of resistance of cultivars.

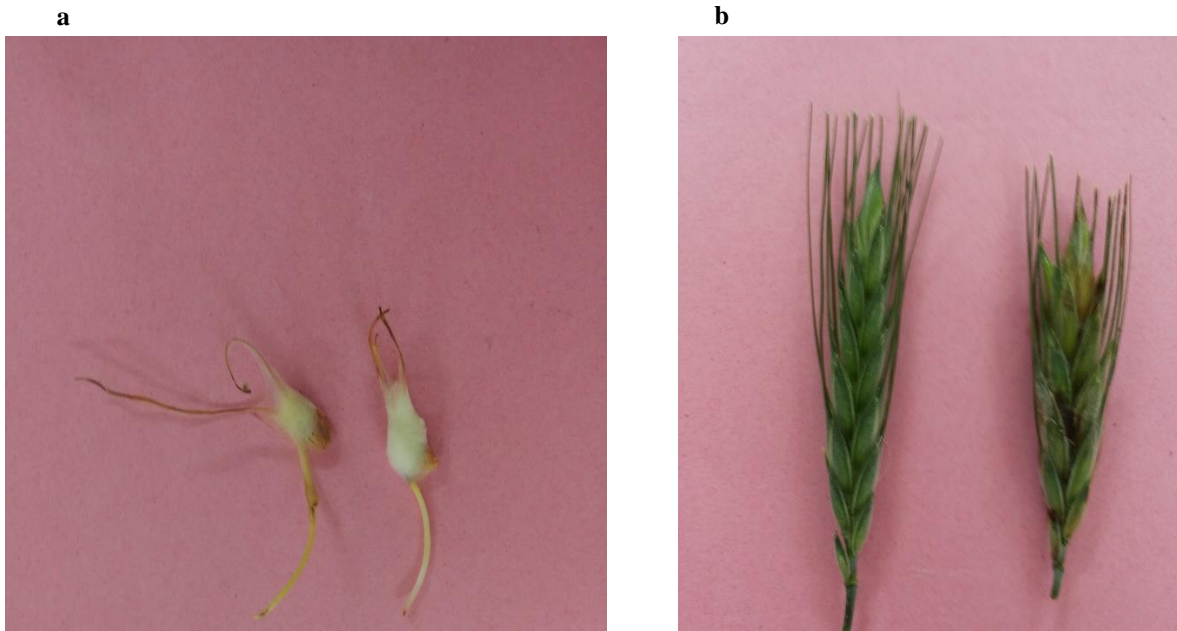
## 3. Results and discussions

Comprehension of variation in *Fusarium* aggressiveness and cultivar resistance is crucial for development of efficient strategies for breeding wheat and barley cultivars against head blight [5]. It is largely accepted that *Fusarium* resistance can be described as horizontal resistance in terms of Van der Plank [10]; horizontal resistance is not race-specific to the maximum degree evident in vertical resistance as shown in Figure 1 [6]. Confirmation of the presence of stable pathogenic races, i.e., vertical true races, was not observed for the two predominant head blight species, i.e., *F. culmorum* and *F. graminearum*, in bread wheat with FHB symptoms upon artificial infection with *Fusarium* fungi [26]. However, no experimental data if vertical true races in durum wheat and barely following infection with FHB species implicated in this disease complex is available. To fill this gap, we therefore tried to

solve the issue of existence of pathogenic races in bread wheat, durum wheat and barley cultivars exhibiting diverse levels of *Fusarium* resistance when challenged with predominant *Fusarium* species in Syria, a high biodiversity country where most temperate-zone cereal agricultural species originated and were first domesticated [27]. Vertical true races that can specifically invade (i.e. are virulent on) cultivars with certain resistance genes cause the breakdown of that race-specific resistance when they augment to a high percentage of the total pathogen population in the field [6].

It is widely accepted that quantitative resistance of the host plant to fungal infections does not confer complete protection [28], but is considered to be effective against all known races/isolates of the pathogen [29]. Unlike to vertical resistance; Van der Plank [10] identified this vertical resistance as immune to some isolates (races) of the fungus but is completely susceptible to other races. In the present research, no wheat and barley cultivar was completely resistant to *Fusarium* infection in harmony with Van der Plank's [10] concept about quantitative resistance. Compared to the negative water control, wheat and barley plants growing in the presence of 16 *Fusarium* isolates causing head blight under several

experimental conditions showed obvious disease symptoms, proposing a strong impact of *Fusarium* fungi on the growth of small-grain cereals plants across the earliest and latest development stages (Figure 2). In wheat- and barley-FHB relationships, resistant host cultivars show consistent resistance to almost all FHB isolates worldwide, showing none presence of significant *Fusarium* × cultivar interactions [5]. In our investigation, combined analysis of bio-experiments demonstrated that isolate × cultivar interactions were significant (Table 1). Our observations agree with earlier reports that showed a significant interaction between isolates of *Fusarium* pathogens and wheat and barley [12]. In other fungus-host associations such as *Helianthus annuus-Phoma* [30], *Oryza sativa-Magnaporthe grisea* [31] and *Triticum aestivum-Septoria tritici* blotch [32], similar scores have been reported. Our above-mentioned results (Table 1) indicate that these hosts, i.e., wheat and barely, may possess different genes for resistance to the respective *Fusarium* species. However, quantitative resistance stability in the eight tested wheat and barley cultivars to FHB infection was fulfilled over years as well as several experimental conditions, suggesting that quantitative



**Figure 2.** Fusarium head blight symptoms on small (a) and adult (b) plant parts under different experimental conditions

resistance of wheat and barley to *Fusarium* is mainly explained by major quantitative trait loci that confer resistance to all FHB isolates [23]. The constancy of horizontal resistance ratings of cultivars is consistent with a hypothesis that wheat- and barley-*Fusarium* interactions for quantitative resistance were of reduced magnitude [23]. It means that this relationship was unstable over our experiments as observed in previous studies [19, 25, 33]. After additional research in this domain with several wheat cultivars and isolates of *F. culmorum*, van

Eeuwijk *et al.* [25] and Snijders van Eeuwijk [33] agreed with Mesterhazy [19], that, although significant *Fusarium*-host interactions were detectable in the pathosystem, this relationship was unstable over experiments, and only affected the order of cultivars very slightly. In fact, Miedaner *et al.* [34] found in their study about the resistance of four cereal crops (triticale, bread wheat, rye and durum wheat) challenged with FHB fungi that isolate × cereal and isolate × cultivar interactions were not significant.

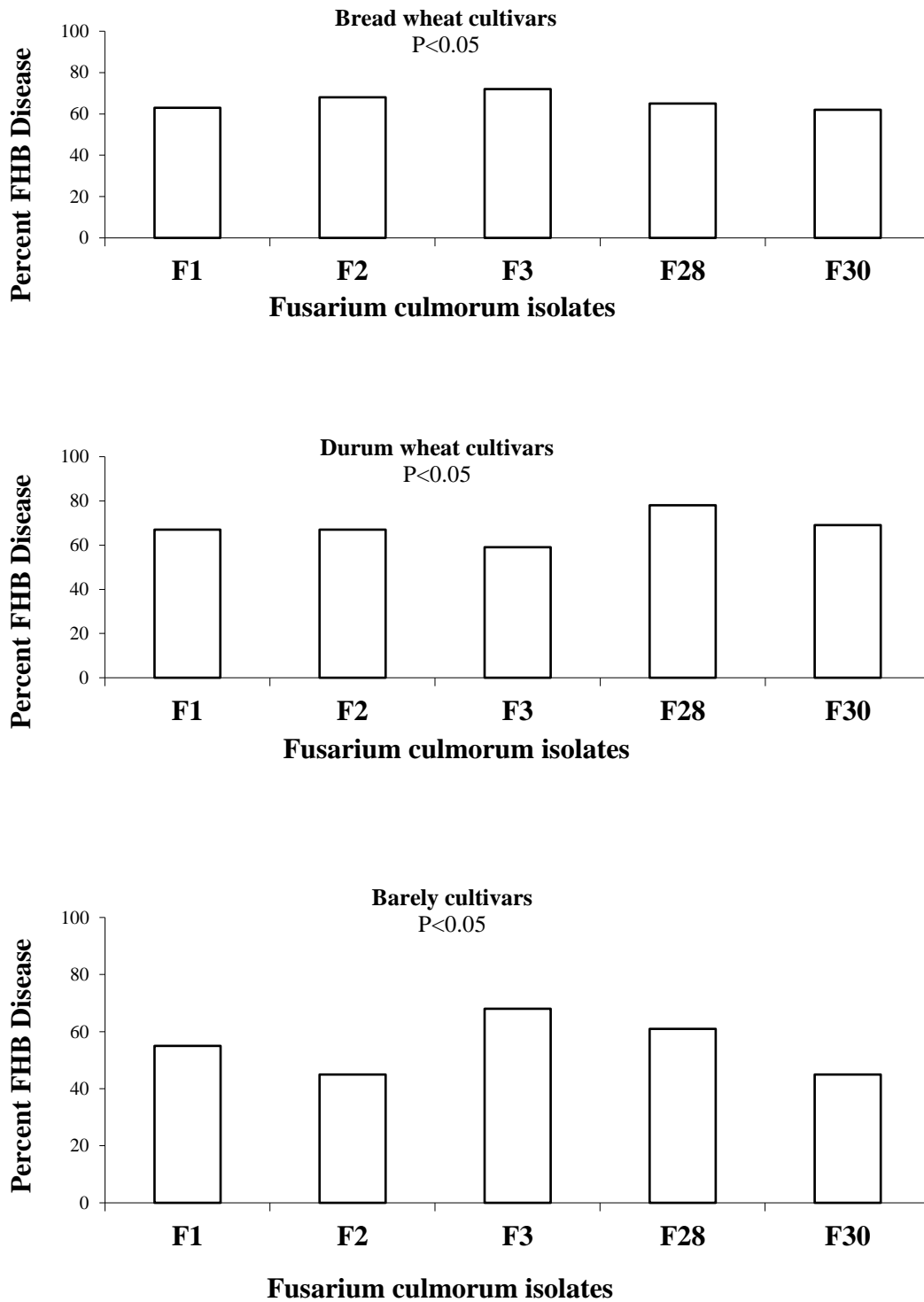
**Table 1.** Analyses of variance for latent period (LP) of detached leaf inoculation, area under disease progress curve (AUDPC) of Petri-dish inoculation and coleoptile length reduction (CL) of a coleoptile infection detected in vitro, disease incidence (DI, Type I) and disease severity (DS, Type II) detected using a detached head test (DHT) under controlled conditions, and disease incidence (DI<sup>CC</sup>, Type I) detected using a head artificial inoculation and disease severity (DS<sup>CC</sup>, Type II) detected using a floret artificial inoculation under controlled conditions in a growth chamber, disease incidence (DI, Type I) and disease severity (DS, Type II) detected using a head artificial inoculation under field conditions (FC) over the three growing seasons (F-test values)

Source of variation	df	LP, AUDPC, CL, DI <sup>DHT</sup> , Type I, DS <sup>DHT</sup> , Type II, DI <sup>CC</sup> , Type I, DS <sup>CC</sup> , Type II, DI <sup>FC</sup> , Type I, DS <sup>FC</sup> , Type II
Cultivar (C)	7	++
Isolate (I)	15	++
C × I	105	++
Error	256	

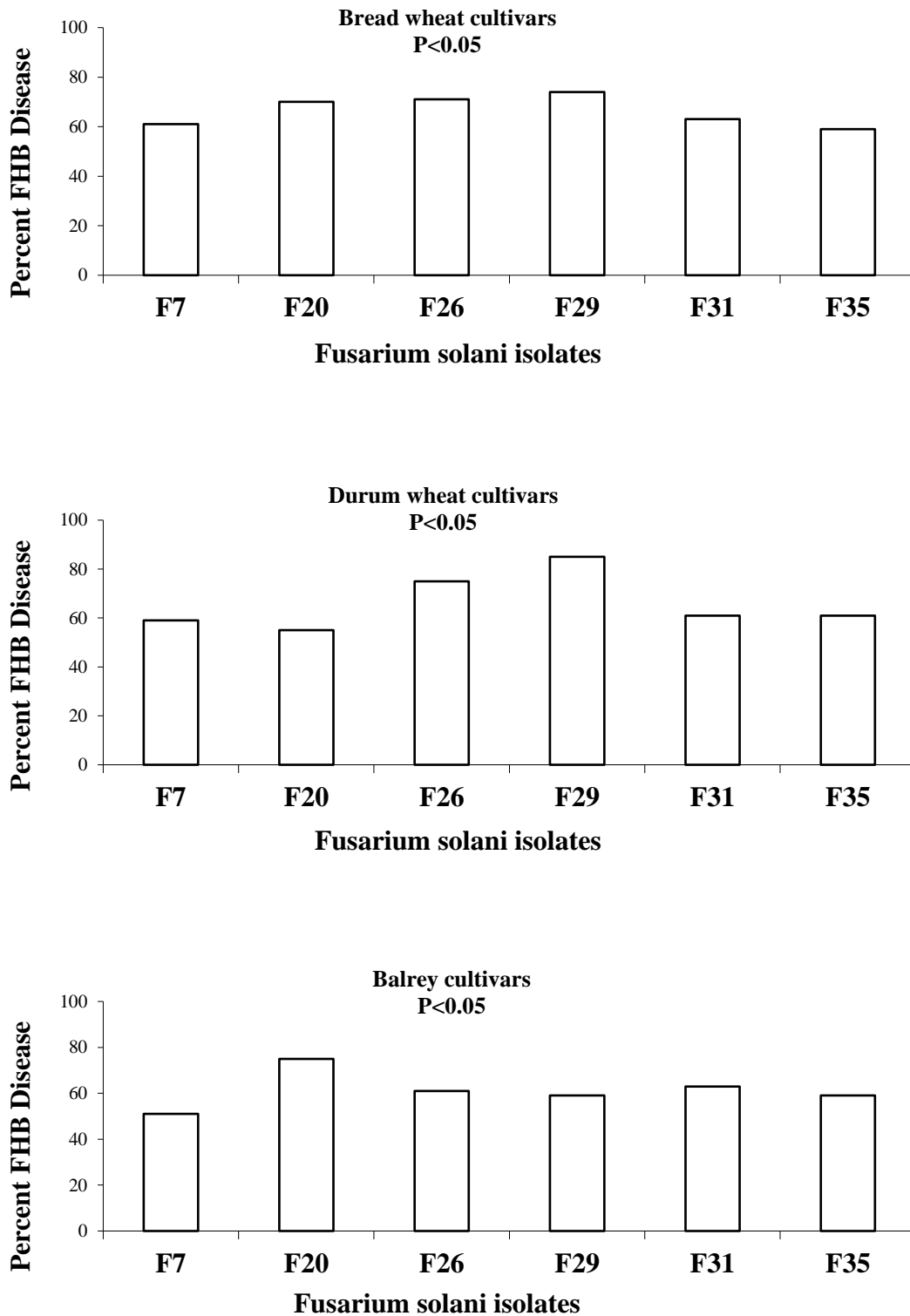
++ – significant at 1% level; df – degree of freedom. Resistance of the eight wheat and barley cultivars infected with *Fusarium* fungi was earlier analyzed and presented by Sakr [23].

Cultivars lacking R genes, or whose R genes were matched by the virulence of the dominant pathogen races, gave less-or- more identical scores of disease when inoculated with diverse races (Figure 1). The estimate of disease could be low or high (Figure 1). Van der Plank [10] claimed that cultivars exhibiting low scores of disease had ‘horizontal resistance’. In the present work, the tested three bread wheat, three durum wheat and two barley cultivars showed consistent resistance to *Fusarium* isolates within each tested species (Figures 3, 4, and 5) and among the four tested *Fusarium* species (Figure 6). In harmony with our data, resistant wheat and barley cultivars show consistent resistance to almost all isolates of *F.*

*graminearum* worldwide [5]. This suggests that our tested species, i.e., *F. culmorum*, *F. solani*, *F. verticillioides*, and *F. equiseti* do not have vertical races. There seems to be no reason for thinking that the resistance to FHB as caused by the four tested species is specific. The same is true for *F. graminearum* and *F. culmorum* infecting bread wheat [22]. Sub-culturing for eight generations of a *Fusarium* isolate did not decrease its capacity to cause FHB [35]. This provided the basis for the conclusion that the resistance to FHB in wheat and barley was of the non-species specific and horizontal type. There was no single for any vertical genes in all tested *Fusarium* pathogens.

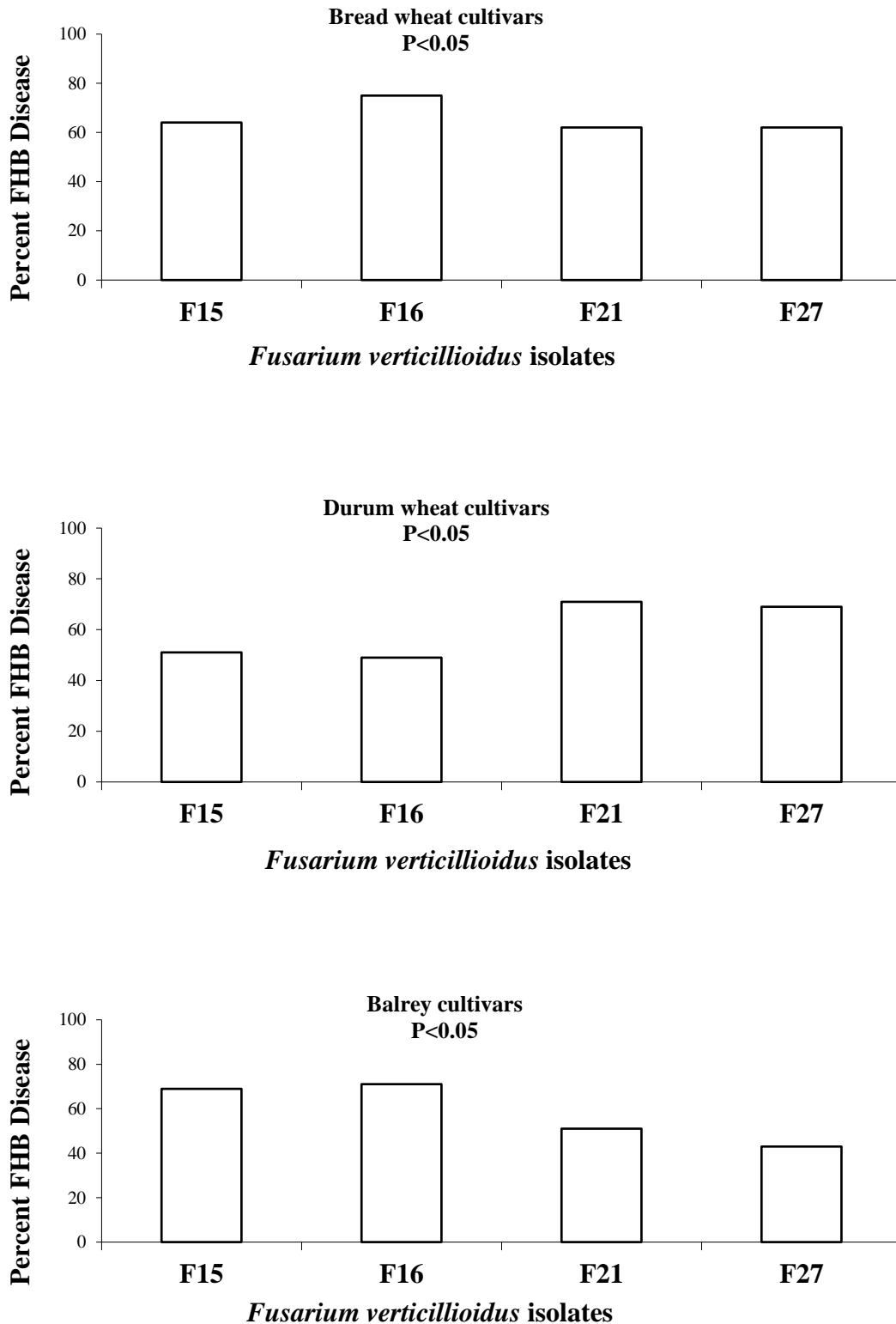


**Figure 3.** Mean values of nine aggressiveness components of five *Fusarium culmorum* causing head blight in three bread wheat, three durum wheat and two barley cultivars. Pathogenic reactions of all cultivars infected with *Fusarium* fungi were previously evaluated according to methods described by Sakr (2023). Significant differences at  $p \leq 0.05$  were observed among the tested cultivars for each cereal species

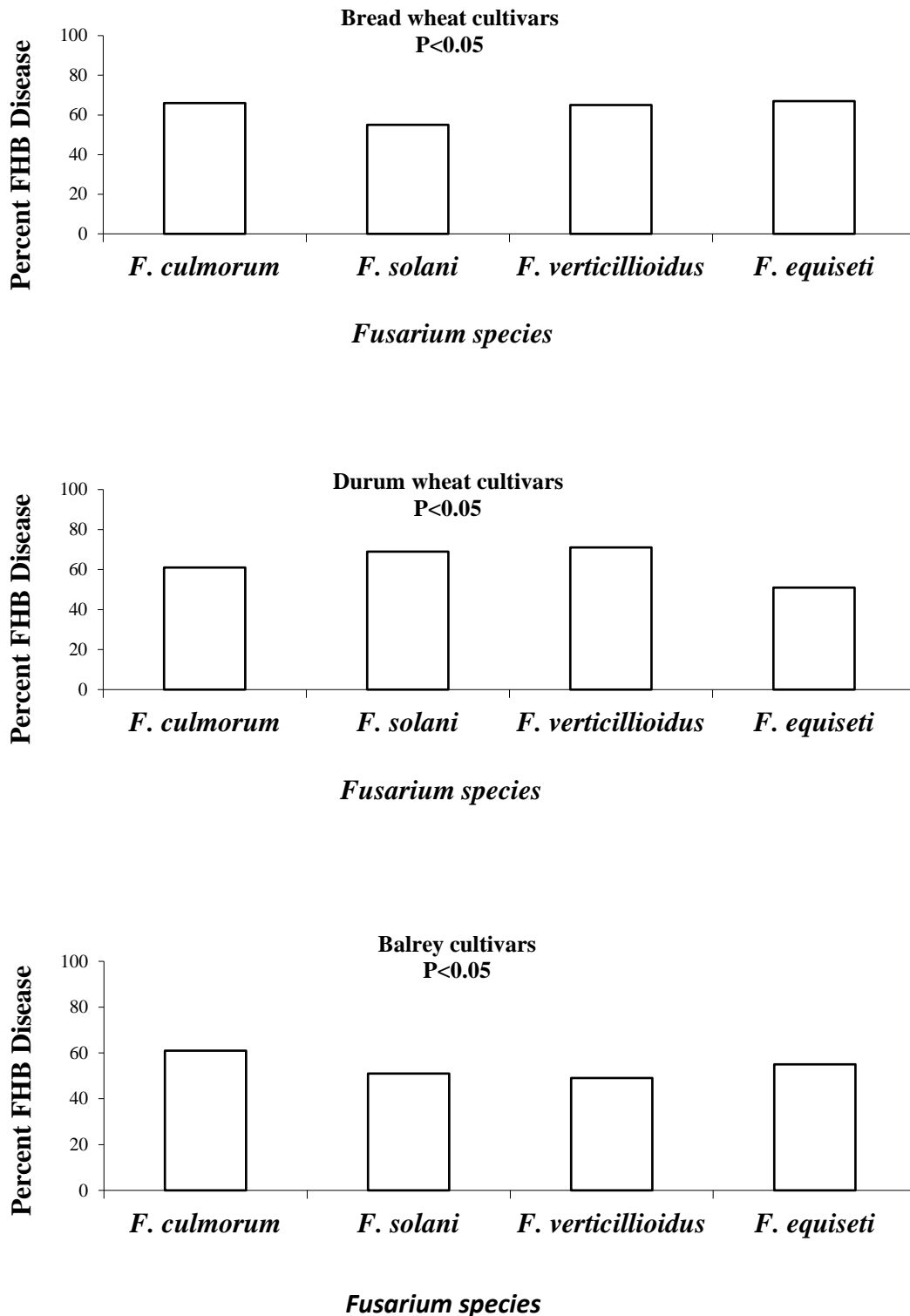


**Figure 4.** Mean values of nine aggressiveness components of six *Fusarium solani* causing head blight in three bread wheat, three durum wheat and two barley cultivars. Pathogenic reactions of all cultivars infected with *Fusarium* fungi were previously evaluated according to methods described by Sakr (2023). Significant differences at  $p \leq 0.05$  were observed among the tested cultivars for each cereal species





**Figure 5:** Mean values of nine aggressiveness components of four *Fusarium verticillioides* causing head blight in three bread wheat, three durum wheat and two barley cultivars. Pathogenic reactions of all cultivars infected with *Fusarium* fungi were previously evaluated according to methods described by Sakr (2023). Significant differences at  $p \leq 0.05$  were observed among the tested cultivars for each cereal species



**Figure 6.** Mean values of nine aggressiveness components of four *Fusarium* head blight, i.e., *F. culmorum*, *F. solani*, *F. verticilliooidus*, and *F. equiseti*, in three bread wheat, three durum wheat and two barley cultivars. Pathogenic reactions of all cultivars infected with *Fusarium* fungi were previously evaluated according to methods described by Sakr (2023). Significant differences at  $p \leq 0.05$  were observed among the tested cultivars for each cereal species

In spite of there is significant interaction between wheat cultivars and *Fusarium* isolates, there is no evidence for stable pathogen races [19, 25], such as are found in small-grain cereal powdery mildew fungi, rust fungi, and some other specialized pathogens. Burgess *et al.* [36] placed isolates of *F. graminearum* (*Gibberella zeae*) into two groups based on whether they were homothallic or heterothallic. Subsequently, Aoki and O'Donnell [37] transferred group 1 to a novel pathogen, *F. pseudograminearum* (*Gibberella coronicola*). Based on the analysis of cultivar resistance to several species of *Fusarium*, Mesterhazy [38] found that resistance to certain isolates of *F. graminearum* as well as to other species of *Fusarium* was not isolate- or species-specific in wheat cultivars. The pathogens of *Fusarium* that cause FHB can infect many other small-grain cereals and maize without exhibiting specialization for any one host, and a host-specific, blight-causing *Fusarium* species has not been reported to date [25]. Thus, the resistance genes in Sumai 3 and other sources presently employed in breeding programs are not expected to succumb to novel *Fusarium* races in the near future [3, 4, 5, 11].

Although the analyzed 16 fungal isolates of the four *Fusarium* species differed largely in quantitative aggressiveness [23], they did not show any evident qualitative differences in virulence. Since the pathogenic specialization can be identified as low [35], wheat and barley breeding for general *Fusarium* resistance may be possible [18, 19, 25]. When the specialized races are absent, the aggressiveness variations between isolates affect resistance distinguishing; at higher aggressiveness, the distinguishing is much better [4]. The *Fusarium* resistance is race non-specific and probably species non-specific [22]. This forecasts durable and stable resistance for extent duration. The only danger is the selection of more aggressive FHB isolates in outbreak centers. In the Chinese Yangtze valley, an augmentation in the more aggressive isolates from the *F. graminearum* clade was reported [5], which can jeopardize low toxin contamination and resistance. This requires verification in pathogenic *Fusarium* populations. This suggests that a higher resistance not only protects against one FHB

pathogen but can also be efficient against the other *Fusarium* pathogens [25].

## 2. Conclusion

Research on Si treatment for *Triticum* and *Hordeum* FHB disease decrease is its infancy; however, Si may provide an additional component for the control of FHB in wheat and barley, as it ameliorates plant defense reactions. For the first time, our current data indicate that Si nonspecifically affects aggressiveness in FHB pathogens. Our observations show that Si could be a valuable tool in integrated FHB management by suppressing pathogen development on wheat and barley when affected by *Fusarium*. Most importantly, no hazard exists to emergence of Si-resistant pathogen populations upon Si applications on diverse FHB populations. More physiological, cytological and biochemical analyses would be required to explore how Si can enhance small grain-cereal defenses to *Fusarium* invasion. All of these data are promising outcomes for the application of Si as an effective and safe control method against FHB damage.

## Compliance with Ethics Requirements.

Author declares that he respects the journal's ethics requirements. Author declares that that he has no conflict of interest and all procedures involving human or animal subjects (if exist) respect the specific regulation and standards.

**Disclosure statement.** No potential conflict of interest was reported by the authors.

**Acknowledgement:** The author would like to thank Director General of the Syrian Atomic Energy Commission (Dr. I. Othman) and the Head of the Department of Agriculture (Dr. M. Zarkawi) for supporting this project.

## References

1. FAOSTAT., Food and Agriculture Organization of the United Nations (FAO). **2022**, Available from: <http://www.fao.org/faostat/>. [Accessed 15th June 2022].
2. Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., and Nelson, A. The global burden of pathogens and pests on major food crops. *Nature Ecology and Evolution*, **2019**, 3(3), 430-439.
3. Buerstmayr, M., Steiner, B. and Buerstmayr, H.,

- Breeding for Fusarium head blight resistance in wheat—Progress and challenges. *Plant Breeding*, **2020**, 139(3), 429-454.
4. Ma, H. X., Zhang, X., Yao, J. B. and Cheng, S., Breeding for the resistance to Fusarium head blight of wheat in China. *Frontiers of Agricultural Science and Engineering*, **2019**, 6(3), 251–264.
  5. Fernando, W. G. D., Oghenekaro, A. O., Tucker, J. R. and Badea, A., Building on a foundation: advances in epidemiology, resistance breeding, and forecasting research for reducing the impact of fusarium head blight in wheat and barley. *Canadian Journal of Plant Pathology*, **2021**, 43(4), 495–526.
  6. Keane, P. J., *Horizontal or Generalized Resistance to Pathogens in Plants*. In: Plant Pathology, InTech, University Campus STeP Ri, Slavka Krautzeka, **2012**, pp. 327-362.
  7. McDonald, B. and Linde, C., Pathogen population genetics, evolutionary potential, and durable resistance. *Phytopathology*, **2002**, 40(1), 349-379.
  8. Simmonds, N. W. Genetics of horizontal resistance to diseases of crops. *Biological Reviews*, **1991**, 66(2), 189-241.
  9. Cowger, C. and Brown, J. K. M., Durability of quantitative resistance in crops: greater than we know? *Annual Review of Phytopathology*, **2019**, 57, 253-277.
  10. Van der Plank, J. E., *Disease resistance in plants*. Academic Press, USA and UK, Utah and Oxford, **1968**, pp. 1-208.
  11. Dahl, B. and Wilson, W. W., Risk premiums due to Fusarium head blight (FHB) in wheat and barley. *Agricultural Systems*, **2018**, 162, 145–153.
  12. Xue, A.G., Chen, Y., Seifert K., Guo, W., Blackwell, B.A., Harris, L.J. and Overy, D. P., Prevalence of *Fusarium* species causing head blight of spring wheat, barley and oat in Ontario during 2001–2017. *Canadian Journal of Plant Pathology*, **2019**, 41(3): 392–402.
  13. Mesterhazy, A., Gyorgy, A., Varga, M., Toth, B., Methodical considerations and resistance evaluation against *F. graminearum* and *F. culmorum* head blight in wheat. The influence of mixture of isolates on aggressiveness and resistance expression. *Microorganisms*, **2020**, 8, 1036.
  14. Sakr, N., Erosion of quantitative resistance in wheat and barley to Fusarium head blight: gene pyramiding achieves and durability study. *Open Agriculture Journal*, **2022**, 16, e187433152211150.
  15. Arseniuk, E., Goral, T. and Czembor, H. J., Reaction of triticale, wheat and rye accessions to graminaceous *Fusarium* spp. infection at the seedling and adult plant growth stages. *Euphytica*, **1993**,70(3), 175-183.
  16. Tekauz, A., Mueller, E. and Beever, D., *Fusarium* headblight of spring wheat in Manitoba in 1987. *Canadian Plant Disease Survey* **1988**, 68, 51.
  17. Snijders, C. H. A., Interaction between winter wheat genotypes and isolates of *Fusarium culmorum*. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent*, **1987**, 52(3a), 807-814.
  18. Mesterhazy, A., Breeding wheat for resistance to *Fusarium graminearum* and *Fusarium culmorum*. *Plant Breeding*, **1983**, 91(2), 295-311.
  19. Mesterhazy, A. Expression of resistance of wheat to *Fusarium graminearum* and *F. culmorum* under various experimental conditions. *Journal of Phytopathology*, **1988**, 123(4), 304-310.
  20. Snijders, C. H. A., Genetic variation for resistance to *Fusarium* head blight in bread wheat. *Euphytica*, **1990**, 50(1), 171-179
  21. Miedaner, T., Borchardt, D. C. and Geiger, H. H. Genetic analysis of inbred lines and their crosses for resistance to head blight (*Fusarium culmorum*, *F. graminearum*) in winter rye. *Euphytica*, **1993**, 65(1), 123-133.
  22. Mesterhazy, A., What Is Fusarium Head Blight (FHB) Resistance and What Are Its Food Safety Risks in Wheat? Problems and Solutions—A Review. *Toxins*, **2024**, 16, 31.
  23. Sakr, N., Resistance to Fusarium head blight in some Syrian wheat and barley cultivars. *Sarhad Journal of Agriculture*, **2023**, 39(1), 80-94.
  24. Leslie, J. F. and Summerell, A. B., *The Fusarium Laboratory Manual*. Blackwell Publishing Professional, Ames, **2006**, pp. 1–388.
  25. Sakr, N., Conservation of cereal fungi following different methods of preservation for long terms. *Pakistan Journal of Phytopathology*, **2020**, 32(2), 159-168.
  26. van Eeuwijk, F. A., Mesterhazy, A., Kling, C. I., Ruckebauer, P., Saur, L., Burstmayr, H., Lemmens, M., MaurinMand Snijders, C. H. A. Assessing non-specificity of resistance in wheat to head blight caused by inoculation with European strains of *Fusarium culmorum*, *F. graminearum* and *F. nivale*, using a multiplicative model for interaction. *Theoretical and Applied Genetics*, **1995**, 90(2), 221–228.
  27. Ceccarelli, S. and Grando, S., *Barley landraces from the Fertile Crescent: a lesson for plant breeders*. International Development Research Centre, Canada, **2002**, pp. 51-76.
  28. Parlevliet, J. E., Durability of resistance against fungal, bacterial and viral pathogens; Present

- situation. *Euphytica*, **2002**, 124(1), 147-156.
29. Mundt, C. C., Durable resistance: a key to sustainable management of pathogens and pests. *Infection, Genetics and Evolution*, **2014**, 27, 446-455.
  30. Darvishzadeh, R., Poormohammad Kiani, S., Dechamp-Guillaume, G., Gentzbittel, L. and Sarraf, A., Quantitative Trait Loci Associated with Isolate Specific and Isolate Nonspecific Partial Resistance to *Phoma macdonaldii* in Sunflower. *Plant Pathology*, **2007**, 56(5): 855-861.
  31. Zenbayashi-Sawata, K., Ashizawa, T. and Koizumi, S., Pi34-AVRPi34: A New Gene-for-gene Interaction for Partial Resistance in Rice to Blast Caused by *Magnaporthe grisea*. *Journal of General Plant Pathology*, **2005**, 71(6), 395-401.
  32. Chartrain, L., Brading, P. A., Makepeace, J. C. and Brown, J. K. M., Sources of resistance to Septoria tritici blotch and implications for wheat breeding. *Plant Pathology*, **2004**, 53(4), 454-460.
  33. Snijders, C. H. A. and Van Eeuwijk, F.A. Genotype × strain interactions for resistance to Fusarium head blight caused by *Fusarium culmorum* in winter wheat. *Theoretical and Applied Genetics*, **1991**, 81(2), 239-244.
  34. Miedaner, T., Lieberherr, B., Gaikpa, D. S., Aggressiveness of *Fusarium culmorum* isolates for head blight symptoms is highly stable across four cereal crops. *Journal of Phytopathology*, **2021**, 169(6): 387-392.
  35. Bai, G. H. and Shaner, G. Variation in *Fusarium graminearum* and Cultivar Resistance to Wheat Scab. *Plant Disease*, **1996**, 80(9), 975-979.
  36. Burgess, L. W., Dodman, R. L., Pont, W. and Mayers, P., *Fusarium disease of wheat, maize and grain sorghum in eastern Australia*. In: *Fusarium: Disease, Biology, and Taxonomy*, Pennsylvania State University Press, Pennsylvania, **1981**, pp. 64-76.
  37. Aoki, T. and O'Donnel, K., Morphological characterization of *Gibberella coronicola* sp. Nov. obtained through mating experiments of *Fusarium pseudograminearum*. *Mycoscience*, **1999**, 40(6), 443-53.
  38. Mesterhazy, A., The role of aggressiveness of *Fusarium graminearum* isolates in the inoculation tests on wheat in seedling state. *Acta Phytopathologica Academiae Scientiarum Hungarica*, **1981**, 16(3-4), 281-92.