Effects of *Tilletia foetida* on Activities of Three Defense Enzymes in Wheat

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**Abstract**  To reveal the effect of *Tilletia foetida* (Wallr.) Liro on defense enzymes activities in wheat stems, leaves and ears, the cultivar ‘Dongxuan 3’ highly sensitive to wheat common bunt and ‘Yinong 18’/Lankao Aizao 8’ highly resistant to wheat dwarf bunt were used as test materials to study the activities of catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) after 0–6 days of infection by the *Tilletia foetida*. The results showed that the activities of defense enzymes of the two wheat varieties were significantly increased. Except for the increase of CAT activity in the leaves of susceptible varieties, the activities of POD and SOD in stems and spikes of resistant varieties were higher than those of susceptible varieties, and the enzyme activities of resistant varieties lasted for a long time and the change range was more gentle. The activity of defense enzyme in the leaves of the two cultivars was higher than that in the stems and spikes, CAT and POD activity in the spikes showed the earliest peak of enzyme activity. All the three kinds of defense enzymes were correlated with disease resistance of wheat, which could provide theoretical basis for breeding resistance to common bunt of wheat.

**Keywords**  Wheat; *Tilletia foetida*; Catalase (CAT); Peroxidase (POD); Superoxide dismutase (SOD)

Common bunt of wheat, caused by *Tilletia foetida*, is a kind of fungal disease that seriously endangers wheat crops. Grains infected by *Tilletia foetida* are usually full of yellow or dark brown fungal spores with unpleasant fishy smell, and release toxic trimethylamines, which causes huge losses in wheat yield and also severely affects the quality of wheat flour (Mourad et al., 2018).

Studies have shown that after pathogens invade host plants, they will cause a series of defensive reactions in the plants themselves, and then changes in the physiological and biochemical indicators of the plants, and make the plants have resistance (Li et al., 2008). Therefore, the increase in plant defense enzyme activity and the formation of disease-related proteins are one of the important indicators to measure the defense response in plants. At present, people mainly study the mechanisms of plant-induced resistance from disease resistance enzymes or substances. These enzymes mainly include peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) (Li et al, 2013). SOD is the most effective intracellular enzyme in the metabolism of reactive oxygen species, which can catalyze the decomposition of O$_2^-$ into H$_2$O$_2$. The increase and decrease of SOD are usually related to the disease resistance and susceptibility of plants (Gill and Tuteja, 2010). CAT is a type of enzyme that is essential for the removal of reactive oxygen species under stress. It can directly decompose H$_2$O$_2$ into H$_2$O and O$_2$ (Garg and Manchanda, 2009), and the conversion efficiency of CAT is extremely high: one CAT molecule can convert about 6 million H$_2$O$_2$ molecules into H$_2$O and O$_2$ per minute (Sun et al., 2019). POD can catalyze the decomposition of H$_2$O$_2$ into phenolic or amine compounds, and can protect cell membranes from damage through antioxidant effects (Liu et al., 2000). Wang et al. (2015) used different resistant genotypes of sugarcane to study their physiological and biochemical reactions at the initial stage of infection by smut, and found that POD played a protective role in the protection of sugarcane against smut infection. The results showed that the changes of defense enzymes such as CAT, POD and SOD were closely related to the disease resistance of host plants.
Although POD, CAT, SOD and other defense enzymes have been studied in other plant diseases, there has been no report on the infection of wheat by *Tilletia foetida*. In this experiment, the activities of defense enzymes (POD, cat and SOD) in stem, leaf and spike were studied by inoculating different resistant and susceptible wheat varieties with spore suspension of *Tilletia foetida* in order to provide theoretical and data reference for wheat breeding for disease resistance.

1 Results
1.1 Changes in catalase (CAT) activity

The results of the dynamic changes of CAT activity in the stems, leaves and spikes of two susceptible varieties of *Tilletia foetida* (Figure 1) showed that, without inoculation, the CAT activities of stems, leaves and spikes of resistant wheat variety ‘Yinong 18’/Lankao Aizao 8’ were 2.03, 2.64 and 1.01 times higher than those of susceptible variety ‘Dongxuan 3’ respectively. After infection, the CAT activity of the two varieties increased rapidly. The CAT activity of the stem, leaf and spikes of the susceptible variety ‘Dongxuan 3’ reached the peak at 3 days after inoculation, and the treatments were 191.40%, 794.23% and 377.92% higher than the control respectively. Two days after the inoculation, the CAT activity peaks appeared in the stems and spikes of the disease-resistant variety, and the increase in the treatment was 147.23% and 404.31% compared with the uninoculated control. At this time, the CAT activity of the leaves continued to increase. The highest value was reached at 4 days after inoculation, which was 178.35% higher than the uninoculated control. After inoculation, the CAT activities of the stems, leaves and spikes of susceptible varieties all showed a trend of first increasing and then decreasing, and the CAT activities were all leaves>spikes>stems, but the peak period of enzyme activity was different. With the extension of time, after the peak period of enzyme activity, the CAT activity of the three parts of the susceptible variety ‘Dongxuan 3’ decreased rapidly. While the decline of the resistant variety ‘Yinong 18’/Lankao Aizao 8’ was more gentle.

![Figure 1](http://microbesci.mp)  
Figure 1 Effects of *T. foetida* on CAT activity in stems, leaves and spikes of susceptible and resistant wheat varieties  
Note: A: ‘Dongxuan 3’; B: ‘Yinong 18/Lankao Aizao 8’

The CAT activities of the stems, leaves and spikes of different wheat varieties were compared (Figure 2). In the stems, the CAT activities of the resistant varieties before and after the inoculation were higher than those of the susceptible varieties ‘Dongxuan 3’. After 2 days of inoculation, the enzyme activity of resistant varieties increased sharply and reached the peak value of 643.91 U/g • FW, and the difference with the susceptible varieties was very significant (P<0.01). After 3 days of inoculation, the enzyme activities of the two varieties began to gradually decrease. At 5 days, the enzyme activity of ‘Yinong 18/Lankao Aizao 8’ became stable, while the enzyme activity of ‘Dongxuan 3’ continued to decrease. At 6 days, the enzyme activity of resistant varieties was still significantly higher than that of susceptible varieties (P<0.05), which was 1.63 times that of susceptible varieties. In the leaves, the CAT activity of the susceptible variety ‘Dongxuan 3’ before inoculation was significantly lower than that of ‘Yinong 18/Lankao Aizao 8’ (P<0.01) (Figure 2B), and after inoculation 1~2 d, the CAT activity of the leaves of
the two varieties gradually increased. At 3d, the activity of CAT in leaves of ‘Dongxuan 3’ reached the peak, which was 1.33 times as much as that of resistant cultivar under the same treatment time, and there was a significant difference between them (P<0.01). Then, the activity of CAT in leaves of susceptible varieties decreased. At the same time, the enzyme activities of resistant varieties increased gradually, and at 4 d it reached the highest. 5–6 days after inoculation, the leaves enzyme activity of ‘Dongxuan 3’ decreased rapidly by 83.89% and 81.17% compared with that of ‘Yinong 18/Lankao Aizao 8’, reaching extremely significant levels (P<0.01). In the spikes, there was no significant difference in enzyme activity between the two varieties before inoculation (Figure 2C). On the 2nd day after inoculation, the activity peak of resistant cultivar ‘Yinong 18/Lankao Aizao 8’ was 1.02 times as high as that of ‘Dongxuan 3’ the next day. After 4–6 days of inoculation, the CAT activity in the spikes of the two varieties decreased, and the enzyme activity of resistant varieties was significantly higher than that of susceptible varieties. Among them, the enzyme activity of ‘Dongxuan 3’ The decrease was more obvious than that of ‘Yinong 18/Lankao Aizao 8’, and the decrease was 2.96 times that of the disease-resistant varieties.

1.2 Changes in peroxidase (POD) activity

Before inoculation, the POD activities of the leaves and spikes of the resistant varieties were higher than those of the susceptible varieties, which were 3.66 and 2.14 times that of ‘Dongxuan 3’ respectively (Figure 3). After inoculation, the enzyme activity changed similarly, all showed a trend of rising first and then falling, which was more obvious than the uninoculated control. At 2 days after inoculation, the stems and leaves of the susceptible variety ‘Dongxuan 3’ reached the peak of enzyme activity, which was 80% and 824.45% higher than the control, respectively. The leaves of the disease-resistant variety ‘Yinong 18/Lankao Aizao 8’ The POD activity rose to the highest value, and the increase was 86.89% compared with the uninoculated control. The POD activity in the spikes of susceptible and resistant varieties reached the peak after 3 days inoculation, which was 941.53% and 661.84% higher than those of the control, respectively. The POD activity of the stems of the resistant variety continued to increase, and reached the maximum value at 4 days after inoculation, and the increase range was 317.75% compared with the control. After inoculation, the POD activity of each organ was leaves>spikes>stems. At the late stage of inoculation, the dynamic change trend of resistant varieties was more stable than that of susceptible varieties.

![Figure 2 Comparison of CAT activity in stems, leaves and spikes of different wheat varieties](image)

Note: A: Comparison of CAT activity in stems of different wheat varieties; B: Comparison of CAT activity in leaves of different wheat varieties; C: Comparison of CAT activity in spikes of different wheat varieties; **: Under the same treatment time, significant differences between different varieties (ANOVA, P<0.01); *: Under the same treatment time, significant differences between different varieties (ANOVA, P<0.05)
Figure 3 Effects of *T. foetida* on POD activity in stems, leaves and spikes of susceptible and resistant wheat varieties

Note: A: ‘Dongxuan 3’; B: ‘Yinong 18/Lankao Aizao 8’

The POD activity of susceptible varieties was significantly higher than that of resistant varieties (P<0.01) at 0–2 days after inoculation (Figure 4A), and reached the peak at 2 days, which was 71.82 U/g • FW. At 3 days, the enzyme activities of susceptible varieties decreased rapidly. Meanwhile, the enzyme activities of resistant varieties continued to increase and were significantly higher than those of susceptible varieties, and reached the peak of 69.97 U/g • FW at 4 days after inoculation.

Compared with susceptible varieties, POD activity of resistant cultivar ‘Yinong 18/Lankao Aizao 8’ increased steadily at first and then decreased slowly. In the leaves, the POD activity of resistant cultivar ‘Yinong 18/Lankao Aizao 8’ was significantly higher than that of susceptible cultivar (Figure 4B), which was 3.59 times of that of ‘Dongxuan 3’. Then, the enzyme activity of leaves of the two varieties gradually increased, and reached the peak at the second day of inoculation. The enzyme activity of ‘Dongxuan 3’ was slightly higher than that of the resistant variety, but there was no significant difference between them. The POD activity of the leaves of the two varieties decreased after 3–6 d inoculation, and the decrease of the susceptible varieties was more obvious by 823.19%. The POD activity of ‘Yinong 18/Lankao Aizao 8’ was significantly higher than those of ‘Dongxuan 3’ at 6 days after inoculation, which was 3.07 times higher than that of susceptible varieties. In the spikes, the dynamic change trend of the spike enzyme activity of the two varieties was consistent before and after inoculation (Figure 4C). The enzyme activity of the resistant variety was significantly higher than that of the susceptible variety in the rising and falling process. The peak of enzyme activity appeared in the spikes of the two varieties after 3 days of inoculation, and there was no difference in the significant level. At 4–6 days after inoculation, the POD activity of the spikes of the susceptible variety ‘Dongxuan 3’ decreased sharply. The decline was 3.33 times that of the disease-resistant variety ‘Yinong 18/Lankao Aizao 8’.

1.3 Changes in superoxide dismutase (SOD) activity

The dynamic changes of SOD activity of the susceptible variety ‘Dongxuan 3’ and the resistant variety ‘Yinong 18/Lankao Aizao 8’ before and after inoculation with the treatment time (Figure 5). When ‘Dongxuan 3’ was not inoculated, there was little difference in SOD activity in the three parts of stems, leaves and spikes. The comparison of SOD activity in each organ of disease-resistant varieties was leaves>stems>spikes. After the inoculation, the enzyme activity of the stems, leaves and spikes of the susceptible varieties increased first and then decreased. The stems reached the peak of enzyme activity before the leaves and spikes, and the growth of the three organs was 85.47%, 217.06% and 161.39%, respectively. The SOD activity of stems and leaves of resistant varieties increased first and then decreased. However, there were two peaks in spikes, which showed a double peak curve of rising, decreasing, rising and decreasing again.
One day after inoculation, SOD activity in the stem of the susceptible variety 'Dongxuan 3' increased rapidly (Figure 6A) and reached a peak of 109.42 U/g * FW, which is different from the enzyme activity of the resistant variety, it reached a very significant level (P<0.01), which was 1.44 times that of resistant varieties. At 2 days after inoculation, the SOD of the stems of the susceptible varieties began to decrease, while the enzyme activity of the resistant varieties rose to the maximum, which was 1.66 times that of the susceptible varieties and was extremely significantly higher than that of the susceptible varieties. 3–6 days after inoculation, the activity of SOD in the stems of resistant varieties began to decline, and the activities of the two varieties gradually approached those before inoculation. In the leaves, before inoculation, the SOD activity of the disease-resistant variety 'Yinong 18/Lankao Aizao 8' was significantly higher than that of the susceptible variety 'Dongxuan 3' (P<0.01) (Figure 6B), 1 to 2 days after inoculation, the enzyme activity of the resistant varieties increased, and the increase rate of the susceptible varieties was 2.54 times faster than that of the resistant varieties. After 3 to 6 days of inoculation, SOD in the leaves of the two varieties the activity gradually decreased, the enzyme activity of disease-resistant varieties continued to be higher than that of susceptible varieties, and the decline of susceptible varieties was higher than that of resistant varieties, which was 1.91 times that of resistant varieties. In the spikes, before inoculation, there was no significant difference in the SOD activity of the spikes of the two susceptible varieties. After the inoculation, the enzyme activity of the spike of the susceptible variety ‘Dongxuan 3’ increased sharply (Figure 6C), until 2 days after the inoculation, Reaching the peak of enzyme activity and extremely significantly higher than disease-resistant varieties. The SOD activity of the spikes of disease-resistant varieties increased rapidly and reached the peak 1 day after inoculation. After 1 day, the SOD activity of the spikes began to decrease,
but at 4 days after inoculation, the SOD activity of the disease-resistant varieties increased rapidly again and reached the peak, at this time the enzyme activity increased by 106.51%. After 5–6 days of inoculation, the SOD activity of the spikes of susceptible varieties decreased, and the enzyme activity of resistant varieties was always higher than that of susceptible varieties.

Figure 6 Comparison of SOD activity in stems, leaves and spikes of different wheat varieties
Note: A: Comparison of SOD activity in stems of different wheat varieties; B: Comparison of SOD activity in leaves of different wheat varieties; C: Comparison of SOD activity in spikes of different wheat varieties

2 Discussion
Plants produce a large number of reactive oxygen species (ROS) during their interactions with pathogens, which play an important role in plant signal transduction and regulation of various cell processes (Qi et al., 2017). However, when too much reactive oxygen species cannot be removed in time, it will be transformed into free radicals that have toxic effects on cells. When it cannot be cleared in time, it will turn into free radicals that are toxic to cells. In order to prevent excessive active oxygen from causing damage, plants have formed and constructed a series of complex enzyme and non-enzymatic antioxidants during long-term evolution (Qin, 2002), including reactive oxygen scavenging enzymes such as CAT, POD and SOD. SOD plays a vital role in scavenging free radicals and is the first line of defense of the active oxygen scavenging system (Jiang et al., 2016). CAT and POD are important H2O2 scavengers in plant tissues, which help metabolize H2O2 into oxygen and water (Li and Yi, 2012).

Huang et al. (2007) studied the dynamic changes of defense enzyme activities of Alfalfa with different resistance after aphid stress. The results showed that the activities of SOD and POD of susceptible varieties maintained an upward trend, while CAT activity showed an alternate increase and decrease. This may be because after adversity stress, the content of salicylic acid increases and binds to salicylic acid binding protein 1, which changes the conformation of CAT and inhibits CAT activity, thereby increasing the H2O2 content that is conducive to disease resistance (Chen and Klessig, 1991), but the plant's own resistance response will inevitably induce an increase in CAT activity, leading to the phenomenon of alternating rise and fall in CAT activity. In this study, the leaves CAT activity of susceptible varieties increased higher than that of resistant varieties after inoculation. This may be due to the presence of complex defense mechanisms similar to the above in the host. At the same time, Li (1982, Guizhou Agricultural Sciences, 2: 40-45) It is believed that the increase in susceptible strains of wheat leaves infected by pathogenic bacteria is higher than that of disease-resistant strains, which may be due to the fact that disease-resistant varieties rely more on increasing polyphenolase activity to resist pathogens. Studies have shown that after wheat seedlings are inoculated with wheat powdery mildew, the activity of defense enzymes in the wheat is positively correlated with resistance (Han et al., 2016). In other words, the stronger the resistance, the stronger the defense enzyme activity, which is different from the research results of CAT activity in leaves in this experiment. However, some studies also showed that there was no positive correlation between defense enzyme
activity and resistance. For example, Gao et al. (2012) found that POD activity in leaves of jujube, grape and peach increased which were harmed by *Apolygus lucorum*, while SOD activity in cherry leaves increased. It has declined. In this study, the peak of SOD and POD activities in all organs of resistant varieties were higher, which indicated that resistant varieties could respond sensitively to pathogen stress.

In this experiment, the defensive enzyme activity of three parts of wheat was measured, and it was found that the defensive enzyme activity of the leaves of susceptible and resistant varieties was higher than that of the other two parts, whether it reached the peak before or after inoculation. The activity of cat and SOD in spikes were more sensitive than POD activity after inoculation, in other words, the peak of enzyme activity appeared earlier, and the peak time of spikes enzyme activity of resistant variety was earlier than that of susceptible variety, and the maximum enzyme activity appeared in 1–2 days after inoculation, while the three defense enzyme activities of stems after inoculation were lower in both susceptible and resistant varieties. In reports on spike diseases, predecessors generally used the leaves of host plants to determine enzyme activity (Wu et al., 2010; Jiang et al., 2014; Zhou et al., 2016), however, the changes of defense enzyme activities in spikes were not known, this study measured the defensive enzyme activity in the spikes and found that the enzyme activity in the spike is more sensitive. This may be due to the fact that the main damage to the wheat spikes by the pathogen caused the spike defense enzyme activities to increase in advance when the pathogen infected the grains.

In this study, the change trend of resistant varieties is more stable than that of susceptible varieties, which is consistent with the previous research results (Jiang, 2010; Wang, 2010), indicating that resistant varieties will resist the occurrence of diseases through stable and sustained defense enzyme activities. This study will provide information for further study on the interaction between *Tilletia foetida* and its host, and provide a theoretical basis for wheat disease resistance research and breeding.

3 Materials and Methods
3.1 Test materials
The high-susceptibility wheat bunt smut variety ‘Dongxuan 3’ and the high-resistance wheat dwarf bunt smut variety ‘Yinong 18/Lankao Aizao 8’ and *Tilletia foetida* (Wallr. Liro), all provided by the Wheat Fungus Disease Research Group, Institute of Plant Protection, Chinese Academy of Agricultural Sciences. ‘Yinong 18/Lankao Aizao 8’ is a hybrid line with ‘Yinong 18’ and ‘Lankao Aizao 8’ as parents. Cultivar culture: the vernalization wheat seedlings were planted in a 25 cm diameter flowerpot with 10 plants in each pot. The seedlings were cultured in biochemical incubator with light intensity of 300 μmol·m⁻²·s⁻¹.

3.2 Cultivation of the inoculum
The spores were made into a suspension of teliospores of *Tilletia foetida*, and then diluted, the teliospore concentration was adjusted to 10⁶/mL, and then spread on a water agar medium, and all the plates were placed upside down at a relative humidity of 50%, incubate in an incubator at 17 °C for 14 d (Li et al., 2018). Observe the germination of spores at any time and collect hyphae for plant inoculation. When the wheat grew to booting stage, the suspension of infected hyphae was injected into the young spikes with syringe for 6 days. Three parts of wheat stem, leaf and spike were cut before and 0-6 days after inoculation at booting stage to determine the enzyme activity, and each treatment was repeated 3 times.

3.3 Determination of defensive enzyme activity
The determination of CAT and POD activity refers to the method of Xu et al. (2009); the determination of SOD activity refers to the photoreduction method of Zhang et al. (2016) of nitronitroblue tetrazolium chloride (NTP).

3.4 Data analysis
The data obtained in the experiment were organized and graphed using Microsoft Excel 2010, and the significance analysis of differences was performed using SPSS 22 software.
Authors’ contributions
He Ting is the executor of the experimental research, completing the data analysis and writing the first draft of the paper; Liu Taiguo and Chen Wanquan participate in the experimental design; Guo Qingyun and Gao Li are the conceivers and responsible persons of the project, and guide the experimental design, data analysis, and paper writing and revision. All authors read and agree to the final text.

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