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Research Article

Effect of *Fusarium udum* infection on the activity of peroxidase, polyphenol oxidase and phenylalanine ammonia lyase in resistant and susceptible genotypes Pigeon pea

Meet Padhiyar
Department of Biochemistry, College of Basic Science and Humanities Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar (Gujarat), India
Smita Singh*
Department of Biochemistry, College of Basic Science and Humanities Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar (Gujarat), India
Anurag Yadav
Department of Microbiology, CPCA, Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar (Gujarat), India
Ramesh V
Department of Dairy Chemistry, G.N. Patel College of Dairy Science, Kamdhenu University, Sardarkrushinagar Campus (Gujarat), India
Kavin k. Soni
Bio-Science Research Centre, Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar (Gujarat), India
Mit Sathvara
Department of Biochemistry, College of Basic Science and Humanities Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar (Gujarat), India

*Corresponding author. E-mail: smitambc2007@sdau.edu.in

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Abstract
Pigeon pea (*Cajanus cajan* L.) is India's second most important pulse crop after chickpea. It is susceptible to several pathogens, including *Fusarium udum,* which is considered the most important fungal pathogen, causing considerable economic loss in India and worldwide. The present study aimed to evaluate the changes in pathogen-induced enzymes (PIE) in *F. udum* wilt-resistant (ICP-8863, BDN-1 and BDN-2) and susceptible genotypes (ICP-2376 and BAHAR) of pigeon pea after seven days of infection. Fifteen days old seedlings were inoculated with *F. udum* (10^6 spores/ml) using the root-dip method. The wilt incidence was observed after seven days of infection; microscopic examination confirmed the presence of *F. udum* based on its characteristic mycelial pattern and conidial features. Biochemical response was recorded by estimating PIE viz., peroxidase (PO), polyphenol oxidase (PPO) and phenylalanine ammonia-lyase (PAL) in various pigeon pea genotypes after the manifestation of infection. The activity of PIE increased in resistant genotypes, particularly BDN-2, which showed the highest PO activity (1.57-fold), while BDN-1 recorded the highest PAL activity (1.55-fold). Overall, defense enzyme activity was lower in susceptible varieties. These results suggested that biochemical changes recorded in resistant genotypes help restrict the disease during infection.

Keywords: *Fusarium udum*, Peroxidase, Phenylalanine ammonia lyase, Pigeon pea, Polyphenol oxidase

INTRODUCTION

India is the largest producer and consumer of pulses, contributing around 28% of the global production (MoAFW, 2024). Pulses are a crucial source of protein in the predominantly vegetarian Indian diet and hold great significance in sustainable agriculture (Gurusamy *et al*., 2022). Among pulses, pigeon pea (*Cajanus cajan* L. Mill sp.) is the second most important crop after chickpea in India. In 2023–24, the country produced

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approximately 3.4 million tonnes of pigeon pea from 5.05 million hectares with an average productivity of 859 kg/ha (DES, 2024).

However, the low productivity of this crop remains due to various abiotic and biotic stresses. Among them, biotic stress caused by pathogens, insects and other biological agents poses a serious threat to pigeon pea cultivation (Sarkar *et al.,* 2021). Notably, Fusarium wilt caused by the soil-borne fungus *Fusarium udum* Butler, is a major yield-limiting factor among various biotic stresses in pigeon pea. The fungus typically enters the plant through root tips or wounds, often facilitated by nematodes and colonizes the vascular system leading to chlorosis, drooping, vascular discolouration, purple banding on stems and ultimately wilting and death (Ramanagouda *et al*., 2022). The disease becomes more prominent during flowering and podding stages often resulting in significant yield losses (Sandhu *et al*., 2023). The instances of *F. udum* induced wilt are specific to pigeon pea varieties, with genetic variability among isolates contributing to differences in virulence (Sharma *et al*., 2019). However, plants have evolved complex inducible defence mechanisms against pathogen attacks, which triggered upon pathogen recognition. While, some responses are constitutive and non-specific, the majority are induced after recognizing pathogen-associated signals (Kaur *et al.,* 2022). These responses include the synthesis of pathogen-related (PR) proteins and the production of antimicrobial metabolites.

A critical component of the defense response is the activity of specific defense-related enzymes such as peroxidase (PO), polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL), which contribute to structural reinforcement and antimicrobial compound production (Cristiane dos Santos and Franco, 2023). Among them, PO plays diverse roles in plant physiology, including lignin and suberin biosynthesis, auxin regulation, phytoalexin production and reactive oxygen species (ROS) metabolism, all of which help to reinforce plant cell walls and restrict pathogen entry (Mohammadi *et al.,* 2021). Similarly, PPO catalyses the oxidation of phenolics to toxic quinones that inhibit pathogen growth (Dahlem *et al*., 2022; Zhang, 2023). In addition, PAL initiates the phenylpropanoid pathway by converting L-phenylalanine to trans-cinnamic acid, leading to the synthesis of lignin, phytoalexins and salicylic acid an important signalling molecule in systemic acquired resistance (Mishra *et al*., 2024). Besides enzymatic defense, genetic and biochemical differences also determine resistance to Fusarium wilt, particularly in crops such as pigeon pea. Biochemical metabolites, including total sugar, total phenol, flavonoids, and protein, are produced in higher amounts in the wilt-resistant genotype compared to the susceptible genotype. Further, resistance to Fusarium wilt in pigeon pea is governed by specific dominant genes, with resistant varieties showing faster activation of defense responses compared to susceptible ones. Therefore, the present study was undertaken to assess the activity of peroxidase, polyphenol oxidase enzyme and phenylalanine ammonia-lyase in wilt-resistant and susceptible genotypes during pigeon pea - *F. udum* infection. The outcome of this study will help in the comprehensive molecular study of resistant mechanisms in pigeon pea.

MATERIALS AND METHODS

The five Pigeon pea (*Cajanus cajan* L.) varieties, including resistant (ICP-8863, BDN-1, BDN-2) and susceptible varieties (ICP-2376, BAHAR) were used in the present study.

The *Fusarium udum* (FU-5) was isolated and maintained by the Department of Pathology, Pulses Research Station, Sardarkrushinagar Dantiwada Agricultural University (SDAU).

Raising of seedlings

The seeds of pigeon pea genotypes were surface sterilized using 0.2% mercuric chloride solution, followed by washing with sterile distilled water. After sterilization, seeds were sown in sterilized soil in plastic bags (16"×16"× 16").

Preparation of inoculum

Inoculum suspensions of *F. udum* (FU-5) were prepared from 7-day-old cultures grown on potato dextrose agar (PDA) medium (Fig. 1). The mycelial growth was covered with 10 ml of sterile distilled water containing 0.01% (v/v) Tween 20. The *F. udum* culture was inoculated by aseptically rubbing the colonies with a sterile loop. The inoculum concentration was adjusted to between 10^4-10^7 spores per millilitre based on microscopic enumeration (Zdenkova *et al.,* 2024).

Infection of *Fusarium udum* on pigeon pea genotypes by root dip method

Pigeon pea genotypes were infected with *F. udum* using a modified root-dip method described by Reddy *et al*. (2022). The root systems of fifteen-day-old seedlings were gently pulled and rinsed with sterile water. The seedlings' roots were submerged for 20 minutes in suspensions containing 10^4, 10^5, 10^6 and 10^7 spores per millilitre. The infected seedlings were transferred to (16"×16"× 16") wide plastic bags containing autoclaved and moistened soil. The experiments were performed in three replications. The pots were regularly watered as and when required. The wilt incidence was examined and data recorded seven days after transplanting using the formula below:

Wilt incidence (%) = Number of plants showing wilting symptoms/ Total number of plants x 100 Eq.1

Pathogen induced enzymes

Pathogen-induced enzymes including peroxidase (PO), polyphenol oxidase (PPO) and phenylalanine ammonia -lyase (PAL) analyses were carried out from leaves of healthy and infected pigeon pea genotypes.

Antioxidant enzyme extraction

One gram of fresh sample was homogenized in ice-cold 10 mL of 100 mM sodium phosphate buffer (pH 7.0) containing 2 mM EDTA, 4% polyvinylpyrrolidone (PVP-40) and 5 mM β-mercaptoethanol using a pre-chilled mortar and pestle. The homogenate was centrifuged at 10,000 rpm for 10 minutes at 4°C, and the supernatant was used for enzyme activity assays.

Peroxidase assay

The peroxidase (PO) activity was assessed following the procedure described by Yadav and co-workers (2017). The 3 mL reaction mixture consisted of 1.9 mL of 100 mM sodium phosphate buffer (pH 7.0), 0.5 mL of 5 mM guaiacol, 0.5 mL of 5 mM H_2O_2 and 100 µL of sample extract. A blank was prepared by mixing 100 µl of sample extract, 2 ml of 100 mM sodium phosphate buffer (pH 7.0) and 0.5 ml of 5 mM guaiacol without substrate (H_2O_2). The reaction was initiated by the addition of H_2O_2, and the increase in absorbance at 470 nm was recorded every 20-second interval for 3 minutes. The enzyme activity was expressed as a change in absorbance recorded at 470 nm per minute per gram fresh weight (FW) (ΔA/min/g FW).

Polyphenol oxidase (PPO) assay

The PPO activity was measured as per the procedures of Lee *et al.* (2022) with slight changes. The 3 ml of reaction mixture was prepared with 2.6 ml of phosphate buffer solution (0.1 M, pH 6.5), 0.3 ml of 0.1 M catechol as a substrate and 0.1 ml of the enzyme extract. The blank was prepared by dissolving all components without substrate catechol. Catechol was added to a spectrophotometer-equipped cuvette to commence the reaction, and an increase in absorbance was monitored between 0 and 1 minute with a 10-second interval at 30°C. PPO activity was expressed as an increase in absorbance at 420 nm ΔA/min/g FW.

Phenylalanine ammonia lyase (PAL) assay

The PAL activity was measured using the Zhang *et al.,* (2021) method with slight changes. To prepare the extract, 0.2 g of powdered samples were homogenized in a pre-chilled mortar and pestle with 2 ml of extraction solution that contained 50 mM borate HCl buffer (pH 8.5) and 0.04 per cent β-mercaptoethanol. The supernatant was utilized as an enzyme source after the homogenate was centrifuged for 15 minutes at 10,000 rpm and 4°C. The reaction was initiated by adding 0.5 ml of 0.1 M phenylalanine in 0.1 M sodium borate buffer (pH 8.8), 3 ml of 0.1 M sodium borate buffer (pH 8.8) and 0.1 ml of enzyme aliquot. 0.5 ml of 0.1 M phenylalanine, 3 ml of 0.1 M sodium borate buffer (pH 8.8), and 0.1 ml of a denatured enzyme aliquot (heat-treated at 80°C) were added to prepare the blank. For one hour, the reaction mixture was incubated at 37°C. 0.5 ml of 0.5 N HCl was added to stop the reactions, and absorbance at 290 nm was recorded. The activity was expressed as an increase in absorbance at 290 nm ΔA/ml/hr.

Data analysis

Comparison between groups was performed using One -way analysis of variance (ANOVA) followed by Tukey's test to compare all pairs of columns. Significant differences between means were calculated at 95 % level of significance.

RESULTS AND DISCUSSION

Morphological and microscopic characteristics of fungal isolate *Fusarium udum* (FU-5)

The fungal isolate *F. udum* (FU-5) exhibited a colony diameter of 75 ± 5.03 mm after 7 days of incubation at 28°C on PDA medium (Fig. 2). Under microscopic observation, a distinct light pinkish mycelium with a moderately fluffy and irregular growth pattern was noted; the isolate was further confirmed based on the size, shape, septation and colour of the conidia. The macroconidia of the isolate were multicellular, large, elongated and crescent-shaped, with two to four septa, whereas the microconidia were minuscule and rounded to oval in form (Fig. 1). These morphological features are consistent with Sucianto *et al.* (2021), who confirmed *F. udum* is characterized by white hyphae, luxuriant and fluffy mycelial growth.

Effect of inoculum concentration

The effect of different inoculum concentrations of *F. udum* was determined by recording the percent wilt incidence on pigeon pea (Table 1). No wilt symptoms was observed at the lowest concentration (1 × 10^4 spores per millilitre). However, the highest wilt incidence (83.33%) occurred when fifteen-day-old seedling roots were exposed to 1 × 10^7 spores per millilitre for 20 minutes. At this concentration, complete chlorosis of leaves was observed within four days post-inoculation. The next best treatment in order of merit was recorded at 1x10^6 spores per ml inoculum concentration, *i.e.,* 56.66% wilt incidence.

Similar observations were reported by Swett *et al.* (2023), who found that *F. oxysporum* f. sp. *ricini* failed to induce wilt disease at 1x10^4 spores/ml during root dip inoculation standardisation, their study documented wilt incidence ranging from 48.85% (at 1 × 10^4 spores per millilitre) to 100% (at 1 × 10^6 and 1 × 10^7 spores

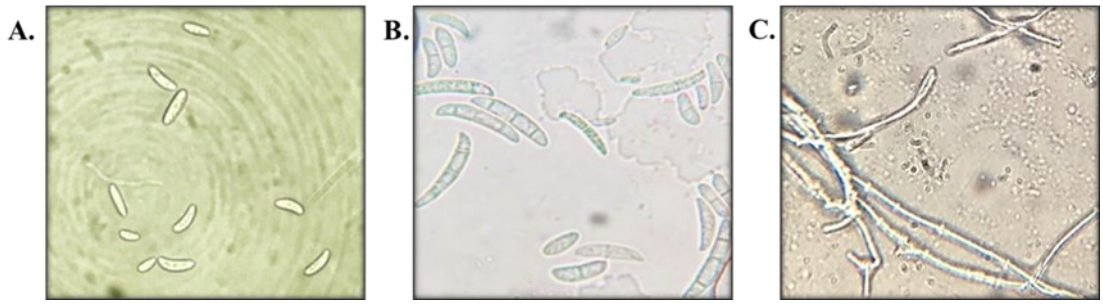

Fig. 1. *Microscopic view of Fusarium udum: (a) Microconidia, (b) Macroconidia, and (c) Mycelia*

per millilitre), with the highest susceptibility observed in fifteen-day-old seedling (55.05%). In another study, Ramanagouda *et al.* (2022) evaluated the effect of Fusarium wilt by infecting plants using the root dip inoculation method, where roots were exposed to a spore suspension (1 × 10^6 spores/ml) for 15 to 20 minutes.

Symptomatology

Wilt symptoms appeared after seven days of infection, manifesting as yellowing, drooping and drying of the leaves. Similar symptoms were reported by Raj *et al*. (2024) noted early leaf yellowing due to chlorophyll degradation under pathogen-induced stress. Infected plants also exhibited interveinal chlorosis, internal browning of the xylem and the appearance of a characteristic purple band extending upwards from the stem base (Sharma *et al*., 2019).

Confirmation of *Fusarium udum* infection

After seven days of infection, characteristic wilt symptoms appeared on the pigeon pea plant. The root, stem and leaf of infected and control plants placed on PDA media and incubated at 27°C showed that white, fluffy growth of the fungus was visible in all the plates containing infected parts of the plant after four days of incubation, indicating *F. udum* as infecting pathogen (Fig. 3). Furthermore, *F. udum* growth was confirmed by microscopic observation of characteristic mycelial patterns and macro and micro conidial features.

Pathogen-induced enzymes activity

The activities of key pathogen-induced enzyme (PIE) in pigeon pea genotypes in response to *F. udum* infection were summarized in Tables 2, 3 and 4. The activities of PIE varied between resistant and susceptible genotypes, reinforcing their importance in managing Fusarium wilt.

Table 1. Effect of inoculum concentration on wilt incidence (%) in pigeon pea

Wilt incidence (%)			
Inoculum concentration (spores/ml)			
1 x 10^4	1 x 10^5	1 x 10^6	1x10^7
00.00 ± 0	16.66 ± 0.34	56.66 ± 0.69	83.33 ± 1.17

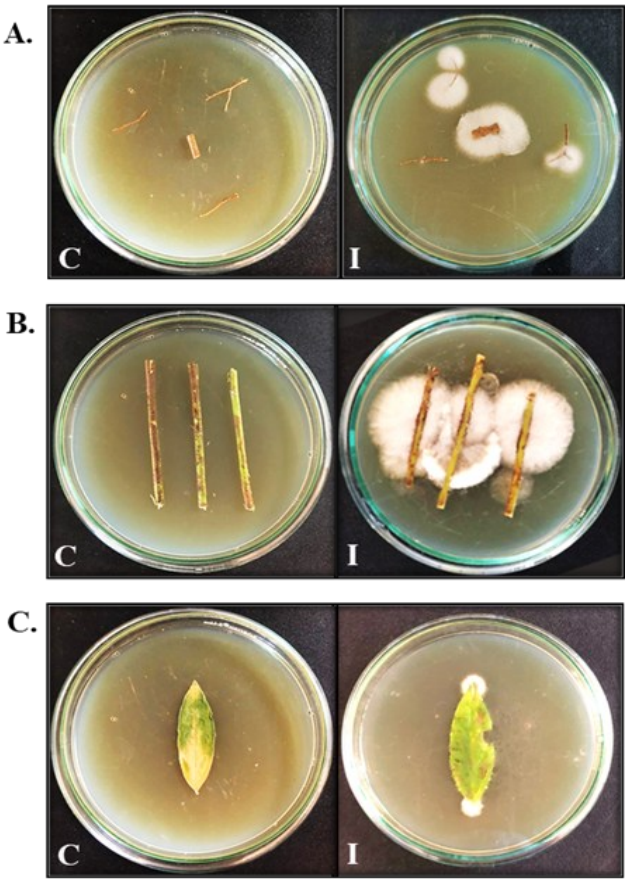

Fig. 2. *Showing various parts of pigeon pea plant on PDA plate: A. Root, B. Stem and C. Leaf, C (Control) and I (Infected).*

Peroxidase (PO), an important antioxidant enzyme known for providing defense to plant; its activity was significantly increased in resistant genotypes after *F. udum* infection. BDN-2 resistant genotype showed highest 1.57-fold increase, whereas susceptible genotypes particularly BAHAR exhibited decline in its activity. These findings align with previous studies by Bisht *et al*. (2024), where PO activity was notably higher in resistant pigeon pea genotypes (WRP-1 and ICP 8863) compared to susceptible ones (T-1515). Similar patterns were observed in tomato, the role of PO as a key defense enzyme across species (Li *et al*., 2021). Another enzyme, polyphenol oxidase (PPO) provides antioxidant defence and pathogen resistance was found to be

Table 2. Peroxidase activity (ΔA $min^{-1}g^{-1}$) in healthy and Fusarium wilt-infected pigeon pea genotypes

Sr. No.	Genotype	Control	Infected	% Change in enzyme activity
Resistant				
1	ICP-8863	4.82 ± 0.19[a]	5.00 ± 0.21[b]	+3.73
2	BDN-1	4.22 ± 0.43[a]	5.92 ± 0.20[b]	+40.28
3	BDN-2	4.68 ± 0.05[a]	7.33 ± 0.24[a]	+56.62
Susceptible				
4	ICP-2376	0.36 ± 0.15[b]	0.39 ± 0.37[c]	+8.33
5	BAHAR	1.07 ± 0.15[b]	0.64 ± 0.68[c]	-40.19
	Average	3.03	3.86	
	S.Em	0.44	0.52	
	CD	1	1.16	
	CV%	3.42	3.86	

*Mean values followed by different letters within the same column are significantly different (p<0.05) (n=3)

Table 3. Polyphenol oxidase activity (ΔA $min^{-1}g^{-1}$) in healthy and Fusarium wilt-infected pigeon pea genotypes

Sr. No.	Genotype	Control	Infected	% Change in enzyme activity
Resistant				
1	ICP-8863	2.07 ± 0.19[ab]	2.59 ± 0.21[ab]	+25.12
2	BDN-1	2.27 ± 0.43[a]	2.88 ± 0.20[a]	+26.87
3	BDN-2	2.16 ± 0.05[b]	2.17 ± 0.24[b]	+0.46
Susceptible				
4	ICP-2376	1.28 ± 0.15[c]	1.12 ± 0.37[c]	-12.50
5	BAHAR	1.80 ± 0.15[b]	1.98 ± 0.68[b]	+10.00
	Average	1.92	2.15	
	S.Em	0.19	0.31	
	CD	0.42	0.69	
	CV%	3.07	3.72	

*Mean values followed by different letters within the same column are significantly different (p<0.05) (n=3)

significantly increased in resistant genotypes. BDN-1 exhibited 1.26-fold increase, while susceptible genotypes specifically ICP-2376 showed a 0.87-fold decrease. Further, the average PPO activity was found to be increased by 17.49% in the resistance genotype, whereas susceptible genotypes exhibited a 1.25% decrease, indicating a less pronounced effect. Therefore, the aforesaid result indicated that higher

PPO activity contributes strong biochemical defense in resistant genotypes against fusarium wilt, whereas lower PPO activity in susceptible genotypes compromises pathogen resistance making them more vulnerable to infection. These results were in agreement with previous studies in lentil, where the activities of PO, PPO and catalase were substantially higher in resistant genotypes (G-13 and G-31) compared to susceptible (G-17). These enzymes play a key role in plant defense mechanisms against *Fusarium* wilt (Rizal *et al*., 2025). Similar defense mechanisms involving key enzymes like PO and PPO were also observed in chilli, where resistant varieties (Pusa Jwala and NP 46-A) showed enhanced enzyme activity compared to the susceptible varieties (S-5 and Ghoomar) when challenged with *Meloidogyne incognita* (Brajnandan *et al*., 2025).

In the plant defense systems, PO and PPO are essential components. Thus, PO strengthens cell walls by

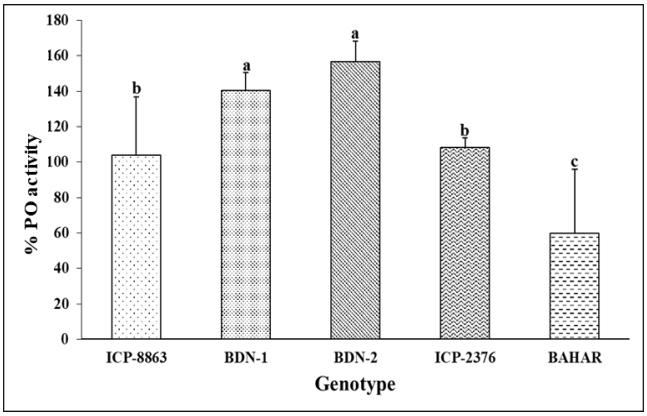

Fig. 3. *Percent peroxidase activity in Fusarium wilt-infected pigeon pea genotypes*

synthesizing lignin and suberin, which strengthens plant defense (Biswas *et al.,* 2020). Furthermore, it increases disease resistance by converting phenolics into toxic quinones and causing oxidative bursts (Wahab *et al.,* 2023). In another study, Jogaiah *et al.* (2020) demonstrated that polyphenol oxidase (PPO) accelerates the conversion of hydroxyphenols into antimicrobial quinones, thereby enhancing plant defense. Similarly, Mohammadi *et al.* (2021) found that resistant pigeon pea genotypes exhibited significantly higher PO and PPO activities, which were linked to reduced oxida-

Table 4. Phenylalanine ammonia-lyase (ΔA $ml^{-1}hr^{-1}$) in healthy and Fusarium wilt-infected pigeon pea genotypes

Sr. No.	Genotype	Control	Infected	% Change in enzyme activity
Resistant				
1	ICP-8863	0.40 ± 0.03^{c}	0.55 ± 0.04^{b}	+37.50
2	BDN-1	0.58 ± 0.05^{a}	0.90 ± 0.10^{a}	+55.17
3	BDN-2	0.48 ± 0.03^{b}	0.62 ± 0.05^{b}	+29.17
Susceptible				
4	ICP-2376	0.37 ± 0.08^{cd}	0.28 ± 0.02^{c}	-24.32
5	BAHAR	0.31 ± 0.01^{d}	0.32 ± 0.03^{c}	+3.23
	Average	0.43	0.53	
	S.Em	0.04	0.05	
	CD	0.09	0.1	
	CV%	2.48	7.22	

*Mean values followed by different letters within the same column are significantly different (p<0.05) (n=3)

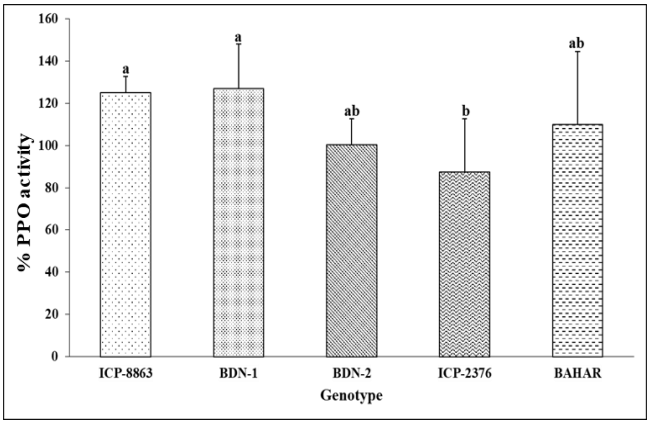

Fig. 4. *Percent polyphenol oxidase activity in Fusarium wilt-infected pigeon pea genotypes*

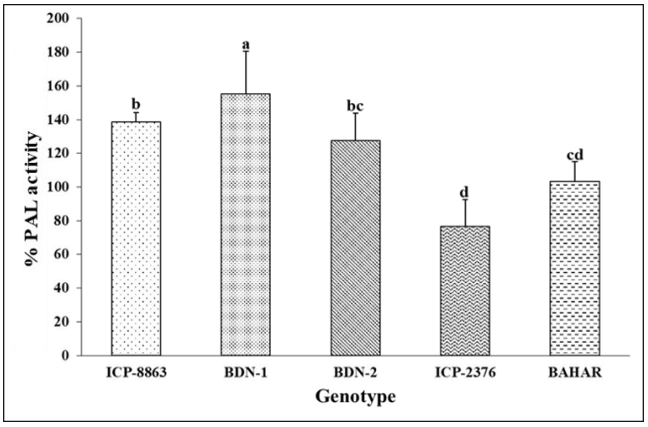

Fig.5. *Percent phenylalanine ammonia lyase activity in Fusarium wilt-infected pigeon pea genotypes*

tive damage and enhanced disease resistance. The antifungal defense mechanisms in plants are intricately associated with the regulation of reactive oxygen species (ROS) by PO and PPO (Mabrouk *et al.,* 2025).

Further, the activity of Phenylalanine ammonia-lyase (PAL) in resistant genotypes exhibited a 40.61% increase; BDN-1 showed 1.55-fold change, while susceptible ICP-2376 displayed the 0.75-fold change. The higher PAL activity in resistant genotypes enhances phenolic accumulation and lignin biosynthesis, reinforcing structural defense and limiting pathogen spread. Conversely, the lower PAL response in susceptible genotypes weakens their structural integrity, making them more vulnerable to infection. The present findings correlated with previous studies, where the resistant pigeon pea genotype ICP 8863 showed elevated PAL activity following *F. udum* infection, while the susceptible genotype ICP 2376 exhibited a decline in PAL activity, this differential response highlights the role of PAL in plant defense against vascular wilt (Purohit *et al.,* 2021). In another study, Ueta *et al.* (2021) demonstrated a similar pattern in Fusarium wilt-resistant chickpeas, where enhanced PAL activity and phenolic accumulation strengthened structural defense.

Conclusion

The activity of pathogen-induced enzymes (PO, PPO and PAL) increased in resistant genotypes. The resistant genotypes, particularly BDN-2, showed the highest PO activity, while BDN-1 recorded the highest PAL activity. Overall, defense enzyme activity was lower in susceptible varieties. This result suggests that the biochemical changes in resistant genotypes help control the disease during infection. The enhanced activity of defence enzymes, *i.e.,* peroxidase (PO), polyphenol oxidase (PPO), and phenylalanine ammonia lyase (PAL) in resistant genotypes of pigeon pea provides resistance against *F. udum* by lignin biosynthesis, phenolic compound accumulation, and oxidative stress management. The increased enzymatic activity in resistant genotypes was also associated with a greater accumulation of toxic quinones and reactive oxygen species (ROS), contributing to pathogen inhibition. The resistant pigeon pea varieties lines reinforce their cell walls through lignin deposition, callose synthesis and cross-linking of structural proteins, forming physical barriers against fungal invasion. Additionally, proteomic studies suggested that specific isoforms of defense-

related enzymes are more active in resistant genotypes, facilitating ROS scavenging and signalling pathways involved in systemic acquired resistance (SAR). Further molecular studies are needed to explore the genetic basis of resistance, which could aid in developing resistant cultivars through advanced breeding and genome editing techniques.

Conflict of interest

The authors declare that they have no conflict of interest.

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